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# Quaestiones entomologicae

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## Editorial — On Finality

Education means, by derivation, “a leading out” (*e* - out, *ducere* - to lead), by implication and usage it means a leading of a person out of the darkness of ignorance into the illumination of knowledge, understanding, and wisdom. Wisdom most importantly, for neither knowledge nor understanding constitute education, though they are essential ingredients of it. Phonograph discs and magnetic tape accumulate knowledge more efficiently than the mind of man; they do not understand, and are wise only in that they start in response to the right stimulus and stop, usually, when they come to the end.

An honest doctor once remarked that birth and death, the two temporal ends of a man, had little finality to them; that while a good doctor was usually pretty certain of a birth when he saw one, most of them were much less certain about the precise moment of death and admitted that the signing of a death certificate brought out the gambler in them. But birth, as the beginning of life, as witness the controversies over abortion, is also at best questionable. So it is with insects; more or less precisely so with such as *Glossina*. At first sight the egg-layers seem to start their lives with more precision, but surely life begins at fertilization, so what of parthenogenesis? Do we go back to the most recent sexually produced individual for the beginning? If a generation runs from fertilization to fertilization, as, in the context of evolution, it must, when we speak of alternation of generations we give it a different meaning. Different by a factor of two. But insect deaths are more dubious. Despite our vast investments in them, they still defy definition; ask any dabbler in the study of median lethal doses. Cryptobiosis and durable diapauses add further doubts.

The ends of an animal in space present problems of a different nature. Animal bodies seem reluctant both to begin and to end. The front end of an animal, that end which (usually) arrives first on the scene in the normal progress of the beast, is analogous to the beginning of life, and, like birth it is usually more clearly defined, more abrupt. But it is rarely completely abrupt; an advance guard of feelers, tentacles, antennae, or pseudopodia precedes the main bulk of the body. The essential quality of a tail is its taper, a reluctance,

as it were, to come to an end. Trailing appendages or receptors often keep it company in its reluctance. Of course a blunt beginning and a tapered finish are the essence of streamlining: some crustacea, unable to face up to this blunt beginning fold their two tapered ends together and allow them to trail behind the superbly rounded bluntness of their folded middles. Even the tails of those of us as have withdrawn them inside in embarrassment, are reluctant to face up to finality. Smaller vertebrae successively succeed each other in what Goethe called a gesture towards infinity. Morphologists recognize the reluctance of segmented animals to start and to finish by giving special names to the first and last pieces of the body, the acron and the telson. These parts really only differ from the segments in between them in having only one neighbour instead of two, and in doing their best to introduce the body and to bring things to an end.

Many forms of life have sidestepped the problem of beginning and ending by adopting a radial rather than a bilateral symmetry. But this only compounds the problem — they have to end in all directions instead of only in two, as witness the tapered arms of starfish. A solution to the problem for bilateral animals which does not appear to have been pursued is to join the two ends together to yield what one might call a ring worm; perhaps dogs and cheese-skippers which chase their tails are playing with this idea. Perhaps the incredible length of some nemertine worms of the genus *Lineus*, the bootlace worms, arises from a simple reluctance to face the problem of ending.

Plants have a masterly way of their own of coming to an end, best shown by trees. Both upwards and downwards, the extremities of these remarkable organisms combine tapering with branching, thus having more and more parts of less and less size until they wind up with a multitude of nothings. As in space, so also in time, plants take on life and give it up with becoming pause.

To return to education, leading out is a gradual process. So is graduation, at least by derivation, though it has become something of a sudden affair.

“Creatures animate with gradual life

Of growth, sense, reason, all summed up in man.”

There are trends in education today divergent from Milton's view; but education — natural education — must be a gradual process, integrated with (and of course embodying the study of) life itself. Despite the element of repetition in it, the term ‘continuing education’ is a valid one, for knowledge grows continually faster and must continue to nourish wisdom. The finality of a final examination is antagonistic to education; life itself is the final examination of wisdom. So also terminal courses; they have no place in education until it is all over. The only truly terminal course is that from the funeral parlour to the graveyard or crematorium. A terminal course with a final examination is the end of everything.

Even an editorial must eventually come to an end. You might think that this is the end. Well, it is. Almost.

Brian Hocking

STUDIES ON BOREAL AGROMYZIDAE (DIPTERA). III.  
PHYTOMYZA MINERS ON CNIDIUM AND CONIOSELINUM (UMBELLIFERAE)

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*Phytomyza sitchensis* n. sp. (type-locality Sitka, Alaska) and *P. conioselini* n. sp. (type-locality Chilkat Peninsula, Alaska) are recorded as miners of *Conioselinum chinense* (L.); and *P. cnidii* n. sp. (type-locality Atkinson Point, Northwest Territories) as miner of *Cnidium cnidiifolium* (Turcz.). No agromyzid miners of these plant genera were previously described.

*Phytomyza sitchensis* n. sp. (localité-type Sitka, Alaska) et *P. conioselini* n. sp. (localité-type Péninsule de Chilkat, Alaska) sont rapportées comme mineuses du *Conioselinum chinense* (L.); et *P. cnidii* n. sp. (localité-type Atkinson Point, Territoires du nord-ouest) comme mineuse du *Cnidium cnidiifolium* (Turcz.). Aucune Agromyzide mineuse de ces genres de plantes n'a été décrite auparavant.

*Phytomyza sitchensis* n. sp. (Fundort vom Typus Sitka, Alaska) und *P. conioselini* n. sp. (Fundort vom Typus Chilkathalbinsel, Alaska) werden als Minierer von *Conioselinum chinense* (L.) besprochen; *P. cnidii* n. sp. (Fundort vom Typus Atkinson Point, Northwest Territories) als Minierer von *Cnidium cnidiifolium* (Turcz.). Agromyziden-Minierer dieser Pflanzengattungen sind bisher nicht beschrieben worden.

In the present paper three new species of *Phytomyza* are described from Alaska and northwest Canada. All belong to the *Phytomyza albiceps* group, in the sense explained in my previous paper (Griffiths, 1972b). These are the first agromyzid species described as miners of *Cnidium* and *Conioselinum*, although there are previous records for Europe of miners which were not bred (see below). Both host-plants of the agromyzid species here described, *Conioselinum chinense* (L.) and *Cnidium cnidiifolium* (Turcz.), occur in north-east Asia, as well as in North America (Hultén, 1968). The former is mainly a coastal plant, ranging on the Pacific coast of North America from the Bering Straits to Washington State; elsewhere it occurs on the eastern seaboard of North America, and in Asia on Hokkaido, Sakhalin, the Kuril Islands and Kamchatka. *Cnidium cnidiifolium* is an arctic plant, not reaching below the 60th parallel in North America; it has an extensive distribution in eastern Siberia, as well as in Alaska, Yukon and along the arctic coast of the Northwest Territories.

The terminology and abbreviations used in my descriptions were explained in the first paper of this series (Griffiths, 1972a). My use of the above plant names follows Hultén (1968). The holotypes of the new species will be deposited in the Canadian National Collection (Ottawa).

#### PREVIOUS RECORDS

An unknown *Phytomyza* species produces linear mines on *Cnidium dubium* (Schkuhr) (= *venosum* Koch) in Poland and Germany. Recorded localities are Crossen-an-Oder (Krosno), Poland (Hering, 1936), Blumerode, Silesia, Poland (viii-ix.1934; Buhr, 1941) and Boizenberg-an-Elbe, Mecklenburg, Germany (Buhr, 1932). Hering (1957:311, no. 1523) describes the mine as follows.

"Channel begins in leaflet-centre, follows first one, then the other leaflet margin, finally filling the entire leaflet; likewise 1-2 further leaflets are mined out; the early channel is finally no longer recognizable. Mine whitish green when fresh, but soon becomes brownish.

Faeces in fine black particles, which in places are linked in beaded fashion, deposited irregularly or in two rows. Semicircular slit on upper surface."

Hering suggests that similar mines in Berlin Botanical Gardens were caused by *Phytomyza mylini* Hering, but this was not confirmed by breeding. Linear mines of the type described are produced on Umbelliferae by many different species of the *Phytomyza albiceps* group. In the absence of any morphological information on larvae or adults, the species concerned cannot be determined.

De Meijere (1937:238) has described and figured a larva collected by H. Buhr from mines on *Conioselinum tataricum* Fisch. at Leningrad (Russia). This larva had only five bulbs on its anterior spiracles, but about 16, arranged more or less in a circle, on its posterior spiracles. This description is not appropriate to the third instar larva of any of the three species found by me on *Conioselinum* in Alaska, for all have more numerous spiracular bulbs. Hering's (1957:315, no. 1546) statement that the mines from Leningrad are "large, taking in a large part of a point of the leaf, only on upper-surface" suggests that they are blotch-mines; but he does not state this explicitly.

### DIAGNOSIS

Caught adults of the *Phytomyza albiceps* group can be reliably identified only by dissection of the male genitalia. Fortunately the form of the aedeagus is strongly differentiated between species of this group, allowing confident identification of many species which are inseparable on external characters. The three new species described in this paper may be included in Spencer's (1969) key to *Phytomyza* species of Canada and Alaska by the extensions given below. The second of these extensions (to couplet 88) incorporates an extension previously proposed by Sehgal (1971).

- 84. Tarsi yellow; aedeagus as Spencer's Figs. 402, 403 ..... *aralivora* Spencer
- Tarsi dark ..... 84a
- 84a. Aedeagus as Spencer's Figs. 473, 474 ..... *osmorhizae* Spencer
- Aedeagus as Fig. 7 ..... *sitchensis* n. sp.
- Aedeagus as Figs. 4, 5 ..... *conioselini* n. sp.
  
- 88. Third antennal segment distinctly enlarged; aedeagus as Spencer's Fig. 468 ..... *nepetae* Hendel
- Third antennal segment not enlarged ..... 88a
- 88a. Aedeagus as Spencer's Figs. 504, 505 ..... *sehgalii* Spencer
- Aedeagus as Sehgal's Figs. 110, 111 ..... *mertensiae* Sehgal
- Aedeagus as Figs. 1, 2 ..... *cnidii* n. sp.

The following key will facilitate identification of mines and immature stages of *Phytomyza* species on *Conioselinum*. No other genera of Agromyzidae are known to attack this plant genus.

#### Key to *Phytomyza* mines on *Conioselinum*

- 1. On *C. tataricum* Fisch. Anterior spiracles of third instar larva (and puparium) with five bulbs; posterior spiracles with about 16 bulbs. .... *P. sp.* (de Meijere, 1937:238)
- On *C. chinense* (L.). Spiracular bulbs of third instar larva and puparium more numerous ..... 2



2. Mine primary blotch (Fig. 14A). Puparium with prominent anal lobes; posterior spiracles of puparium and third instar larva with 21-22 bulbs in broad ellipse (nearly circular) (Fig. 11) ..... *P. sp.* (compare *angelicae* Kaltenbach)
- Mine basically linear, though portions of the channel may coalesce in narrow leaf lobes (Fig. 14B). Puparium without prominent anal lobes; posterior spiracles of puparium and third instar larva with bulbs in narrow ellipse (Fig. 12, 13) ..... 3
3. Puparium smoothly rounded, with intersegmental boundaries scarcely impressed (Fig. 9) ..... *P. sitchensis* n. sp.
- Puparium as Fig. 10, with intersegmental boundaries distinctly impressed ..... *P. conioselini* n. sp.

## TREATMENT OF SPECIES

### *Phytomyza cnidii* new species

*Adult.* — Head with orbits narrowly projecting above eye in lateral view; genae in middle 1/3 to 1/4 of eye height; eyes with only sparse fine pubescence. Frons at level of front ocellus 2-2½ times width of eye. Ors directed posteriorly, ori directed inwardly; posterior ors about 2/3 as long as anterior ors; anterior ori variably developed, ranging from very short to 2/3 as long as posterior ori; orbital setulae few (3-5), in one row. Peristomal margin with vibrissa and 2-3 upcurved peristomal setulae. Third antennal article rounded distally, with short pubescence.

3 + 1 dc; acr in 4-5 rows; 5-10 presutural ia; 4-7 postsutural ia; inner pa about half as long as outer pa.

Second cross-vein (m-m) absent;  $m_{1+2}$  weak, absent from centre of wing in two females (although they retain its terminal portion at wing tip). Costal ratio  $mg_2/mg_4$  2.2-2.4. Wing length 1.8-2.0 mm.

Colour largely dark. Centre of frons dark brown, only slightly paler than black ocellar plate, vertex and orbits; genae brown. Antennae black. Palpi black; labella orange-yellow. Thorax finely grey-dusted, weakly shining, largely black with pale coloration only along notopleural and mesopleural sutures (and in one specimen also at corners of humeral calli); wing base yellow; squamae pale or somewhat infuscated, with dark fringe. Legs largely black, with tips of front femora not contrasting, yellow-brown or red-brown. Basal cone of ovipositor (♀) largely shining, grey-dusted on dorsal surface only narrowly at base.

Male postabdomen with 8th sternum fused with 6th tergum. Telomeres not clearly delimited from periandrium, bearing dense group of setulae. Pregonites inconspicuous (weakly pigmented), extending ventrally, shielding base of aedeagus at rest. Aedeagal hood with two pairs of lateral sclerites. Aedeagus as Fig. 1, 2; basal section with group of very small spinules on dorsal surface between basal sclerites; medial lobe with well-defined loop of sclerotization; distal section largely unpigmented, with distiphallus represented by slender strip of sclerotization. Ejaculatory apodeme as Fig. 3.

*Puparium and third instar larva.* — Mandibles with two alternating teeth; right mandible longer than left. Anterior spiracles with 8-10 bulbs in irregular ellipse. Posterior spiracles on short conical processes, with 14-15 bulbs in narrow ellipse. Puparia dark brown or black, 1.7-1.8 mm long, strongly arched, with clearly impressed intersegmental boundaries; anal lobes weakly developed.

*Mine.* — Larvae leaf-miners on *Cnidium cnidiifolium* (Turcz.), leaving leaf before puparium formation. A description of the mine cannot be given, as the leaves from which the type series was bred decomposed while in transit.

*Types.* — Holotype ♂, 3 ♀♀ paratypes from larvae 26.vii.70 on *Cnidium cnidiifolium* (Turcz.), 4 miles S Atkinson Point (on pingo), Northwest Territories, Canada, emerged 2.v.71, leg. P. G. Kevan.

*Phytomyza sitchensis* new species

*Adult.* — Head with orbits not projecting above eye in lateral view; genae in middle 1/3 to 1/4 of eye height; eyes with only sparse fine pubescence. Frons at level of front ocellus about twice width of eye. Ors directed posteriorly, ori directed inwardly; posterior ors 3/4 to almost as long as anterior ors; anterior ori short or absent; orbital setulae few (4-6), in one row. Peristomal margin with vibrissa and 3-5 upcurved peristomal setulae. Third antennal article rounded distally, with short pubescence.

3 + 1 dc; acr in 3-4 rows; 5-6 presutural ia; 6-7 postsutural ia; inner pa about half as long as outer pa.

Second cross-vein (m-m) absent. Costal ratio  $mg_2/mg_4$  3.4-3.5. Wing length 2.4-2.6 mm.

Colour almost entirely dark. Centre of frons and genae dark brown, scarcely paler than rest of head. Labella orange-yellow. Thorax grey-dusted over black ground colour, only weakly shining, with pale coloration only along notopleural and mesopleural sutures. Wing base and squamae yellowish white, latter with dark margin and fringe. Legs largely dark, with tips of front femora contrastingly yellow; tips of other femora less contrasting, yellow-brown or dark. Basal cone of ovipositor (♀) grey-dusted on about basal third.

Male postabdomen with 8th sternum fused with 6th tergum. Telomeres partly delimited from periandrium by suture on outer side, bearing numerous fine setulae. Pregonites extending ventrally (shielding base of aedeagus at rest), but inconspicuous (weakly pigmented). Aedeagal hood with two pairs of lateral sclerites (the more dorsal pair rather ill-defined). Aedeagus as Fig. 7; right basal sclerite expanded at base; both basal sclerites with row of conspicuous spinules distally above their dorsal margins; medial lobe with pair of slender well-defined sclerites; distal section long, at its base with well-defined sclerite (mesophallus) enclosing ejaculatory duct, largely membranous distally with only weak traces of terminal pigmentation (distiphallus). Ejaculatory apodeme as Fig. 8.

*Puparium and third instar larva.* — Mandibles with two alternating teeth; right mandible longer than left. Anterior spiracles with two short horns, with about 14 bulbs in ellipse. Posterior spiracles on short broad processes, with 26-33 bulbs in long narrow ellipse with wide gap on inner side (Fig. 12). Puparia (Fig. 9) shining black, about 1.7 mm long, smoothly rounded with intersegmental boundaries scarcely impressed; anal lobes absent.

*Mine.* — Larvae leaf-miners on *Conioselinum chinense* (L.). Mine (Fig. 14B) entirely linear, mainly following sinuations of leaflet margins, about 5 cm long, 1-1½ mm wide terminally; faeces deposited as fine particles, mostly close together or forming beaded strips; mine entirely on upper surface of leaf, appearing whitish green in reflected light; larvae leaving leaf through semicircular slit on upper surface before puparium formation.

*Types.* — Holotype ♂, 1 ♀ paratype from larvae 20-30.viii.69 on *Conioselinum chinense* (L.), Starrigavan (on beach), Sitka, Alaska, emerged 11-14.v.70, leg. G. C. D. Griffiths. 1 ♀ paratype from larva 27-30.vi.68 on *Conioselinum chinense* (L.), Chilkat Peninsula (near Haines), Alaska, emerged 23.vii.68, leg. G. C. D. Griffiths.

*Remarks.* — The breeding data given above indicate that *sitchensis* is multivoltine. The smoothly rounded puparia are of the type described by Allen (1957) for *P. obscurella* Fallén and other European species. The other known miners of *Conioselinum* do not have puparia of this type.

*Phytomyza conioselini* new species (♂)

*Adult.* — Head with orbits only very narrowly projecting above eye in lateral view; genae in middle 1/4 of eye height; eyes with only sparse fine pubescence. Frons at level of front ocellus about 2½ times width of eye. Ors directed posteriorly, ori directed inwardly; posterior ors from 2/3 to fully as long as anterior ors; anterior ori 1/2 to 2/3 as long as posterior ori; orbital setulae numerous (8-10), irregularly arranged (a few lying between main row and level of orbital bristles). Peristomal margin with vibrissa and 5-8 upcurved peristomal setulae. Third antennal article rounded distally, with short pubescence.

3 + 1 dc (except 2 + 1 on one side in paratype); acr and ia long; acr in 3-4 rows; 5-9 presutural ia; 4-9 postsutural ia; inner pa about half as long as outer pa.

Second cross-vein (m-m) absent. Costal ratio  $mg_2/mg_4$  3.3. Wing length 2.5 mm.

Colour largely dark. Centre of frons ochreous, somewhat contrasting with dark orbits, ocellar plate and vertex; genae ochreous to yellow-brown. Antennae dark. Palpi black; labella yellow. Thorax strongly grey-dusted, scarcely shining, largely dark with pale coloration only along notopleural and mesopleural sutures and on postalar callus (below outer pa). Wing base and squamae whitish, latter with dark margin and fringe. Legs largely dark, with tips of front femora contrastingly yellow; tips of other femora less contrasting, yellow-brown or reddish.

Male postabdomen with 8th sternum fused with 6th tergum. Telomeres partly delimited from perianthrium by suture on outer side, bearing dense group of fine setulae. Pregonites large, extending ventrally (shielding base of aedeagus at rest), but inconspicuous (weakly pigmented). Aedeagal hood with two pairs of lateral sclerites (the more dorsal pair rather ill-defined). Aedeagus as Fig. 4, 5; basal section without spinules; medial lobe with pair of asymmetrically developed sclerites, that on left side much expanded with projecting point; distal section very short, with complex sclerotization. Ejaculatory apodeme as Fig. 6.

*Puparium and third instar larva.* — Mandibles with two alternating teeth; right mandible longer than left. Anterior spiracles with about 12 bulbs in irregular ellipse. Posterior spiracles (Fig. 13) on short conical processes, with 22-29 bulbs in narrow ellipse. Puparia (Fig. 10) dark brown or black, shining, 2.1-2.2 mm long, strongly arched, with intersegmental boundaries distinctly impressed; anal lobes absent.

*Mine.* — Larvae leaf-miners on *Conioselinum chinense* (L.). Mines linear, similar to those of *sitchensis*; larvae leaving leaf through semicircular slit before puparium formation.

*Types.* — Holotype ♂, 1 ♂ paratype from larvae 27.vi-2.vii.68 on *Conioselinum chinense* (L.), Chilkat Peninsula (near Haines), Alaska, emerged 12-13.x.68, leg. G. C. D. Griffiths.

*Remarks.* — Puparia of this species and of *sitchensis* were obtained from linear mines on *Conioselinum* collected on the Chilkat Peninsula. Unfortunately my records do not enable me to separate the pressed mines according to species. There seems no obvious basis for dividing them into two groups. However, the puparia are readily separable, for those of *conioselini* have impressed intersegmental boundaries (Fig. 10), while those of *sitchensis* are smoothly rounded (Fig. 9).

I do not know whether the late emergence of the two specimens indicates that this species has a second generation in autumn, or was a "forced" emergence caused by delay in my obtaining outdoor storage facilities.

The paratype male has an abnormal abdomen, with incomplete hypopygial rotation. The cause of this was evidently unsuccessful parasitoid attack, for in the abdomen was found a large capsule (0.325 x 0.15 mm) containing a hymenopterous larva. The aedeagus of the paratype agrees with that of the holotype except that the right (not left) sclerite of

the medial lobe is expanded. I interpret its condition as abnormal in this respect, since disturbances of the rotation process in cyclorrhaphous Diptera are often associated with anomalous development of asymmetrical structures.

*Phytomyza* sp. (compare *angelicae* Kaltenbach)

In addition to larvae of *sitchensis* and *conioselini*, I also collected on the Chilkat Peninsula larvae of a third species of *Phytomyza* on *Conioselinum chinense* (L.), these producing primary blotch-mines (Fig. 11, 14A). The mines and puparia of this species are similar to those of *P. angelicae* Kaltenbach (on *Angelica*). Unfortunately I have so far obtained only female flies. These are similar to *angelicae*, differing from the other *Conioselinum*-miners in having a bright yellow frons. I cannot determine whether they represent a distinct species until males are obtained for critical comparison.

#### ACKNOWLEDGEMENTS

I am most grateful to P. G. Kevan for collecting and sending me the material from *Cnidium*. My material from *Conioselinum* was collected on field trips supported by the Boreal Institute of the University of Alberta. My wife Deirdre kindly prepared the illustration of leaf mines (Fig. 14). I am grateful to M. von Tschirnhaus and K. A. Spencer for confirming that none of the species described in this paper was previously known to them.

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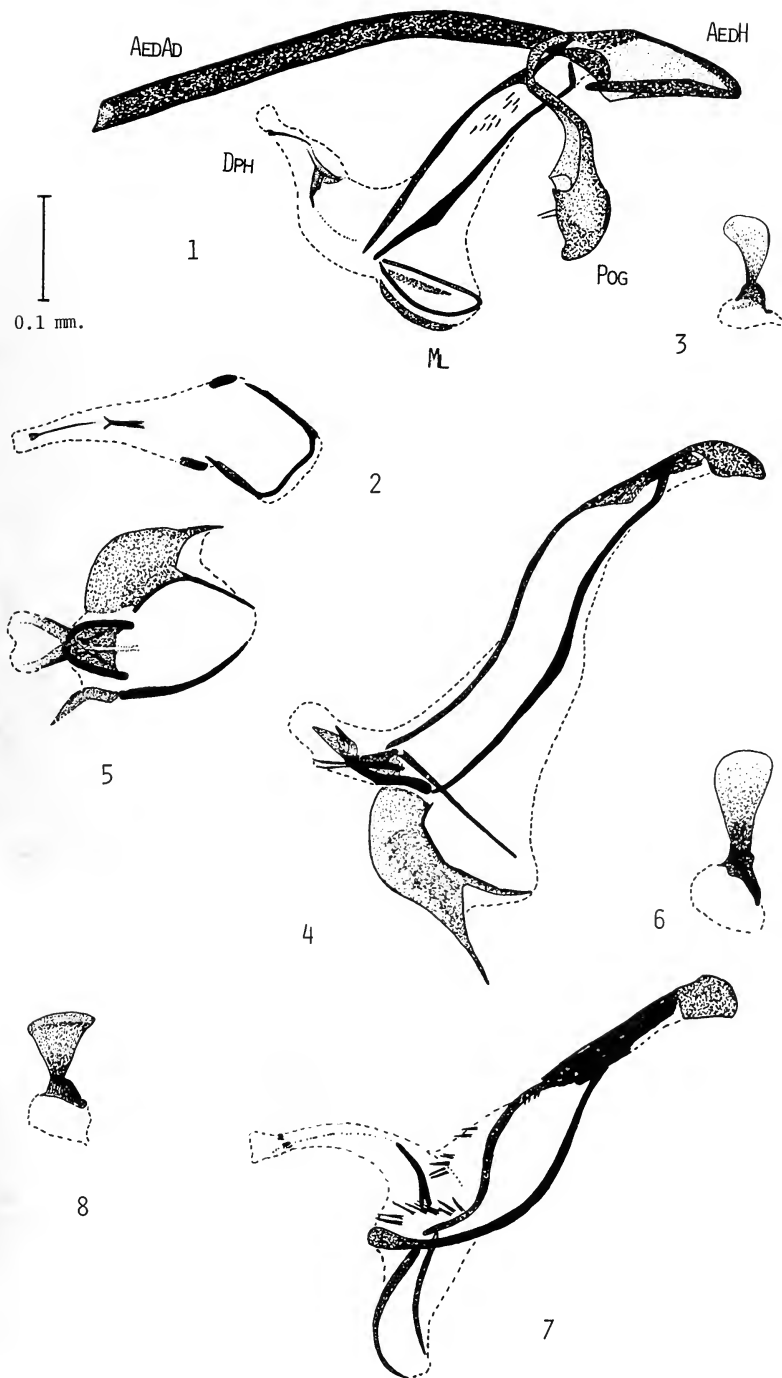


Fig. 1-3. *Phytomyza cnidii* n. sp., holotype ♂: 1, aedeagus and associated structures in lateral view (AEDAD aedeagal apodeme, AEDH aedeagal hood, DPH dististiphallus, ML medial lobe, POG postgonite); 2, distal section and medial lobe of aedeagus in anteroventral view; 3, ejaculatory apodeme. Fig. 4-6. *Phytomyza conioselini* n. sp., holotype ♂: 4, aedeagus in lateral view; 5, distal section and medial lobe of aedeagus in anteroventral view; 6, ejaculatory apodeme. Fig. 7-8. *Phytomyza sitchensis* n. sp., holotype ♂: 7, aedeagus in lateral view; 8, ejaculatory apodeme.

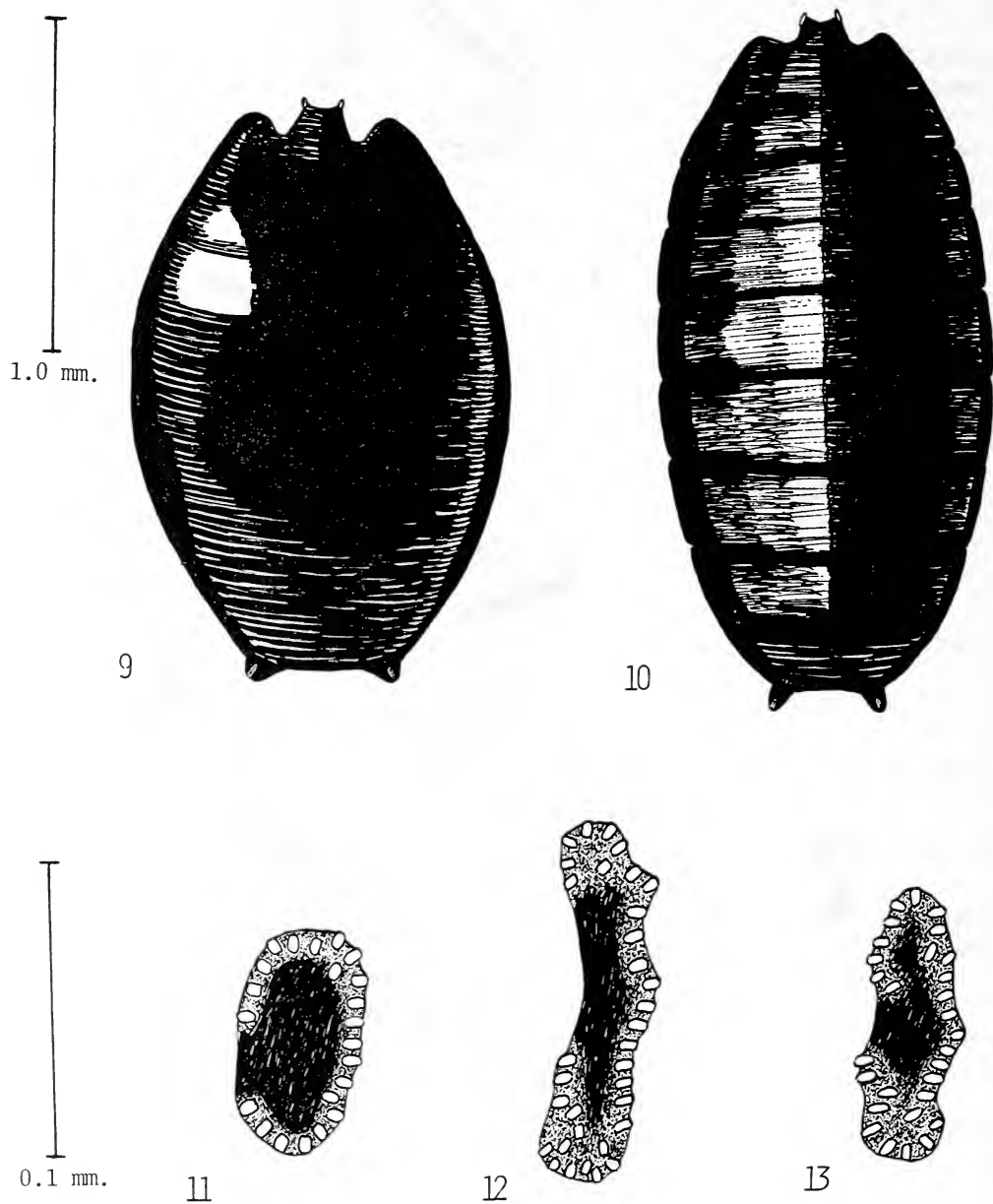


Fig. 9. *Phytomyza sitchensis* n. sp., puparium in dorsal view. Fig. 10. *Phytomyza conioselini* n. sp., puparium in dorsal view. Fig. 11. *Phytomyza* sp. (compare *angelicae* Kaltenbach), posterior spiracle of puparium in caudal view. Fig. 12. *Phytomyza sitchensis* n. sp., posterior spiracle of puparium in caudal view. Fig. 13. *Phytomyza conioselini* n. sp., posterior spiracle of puparium in caudal view.

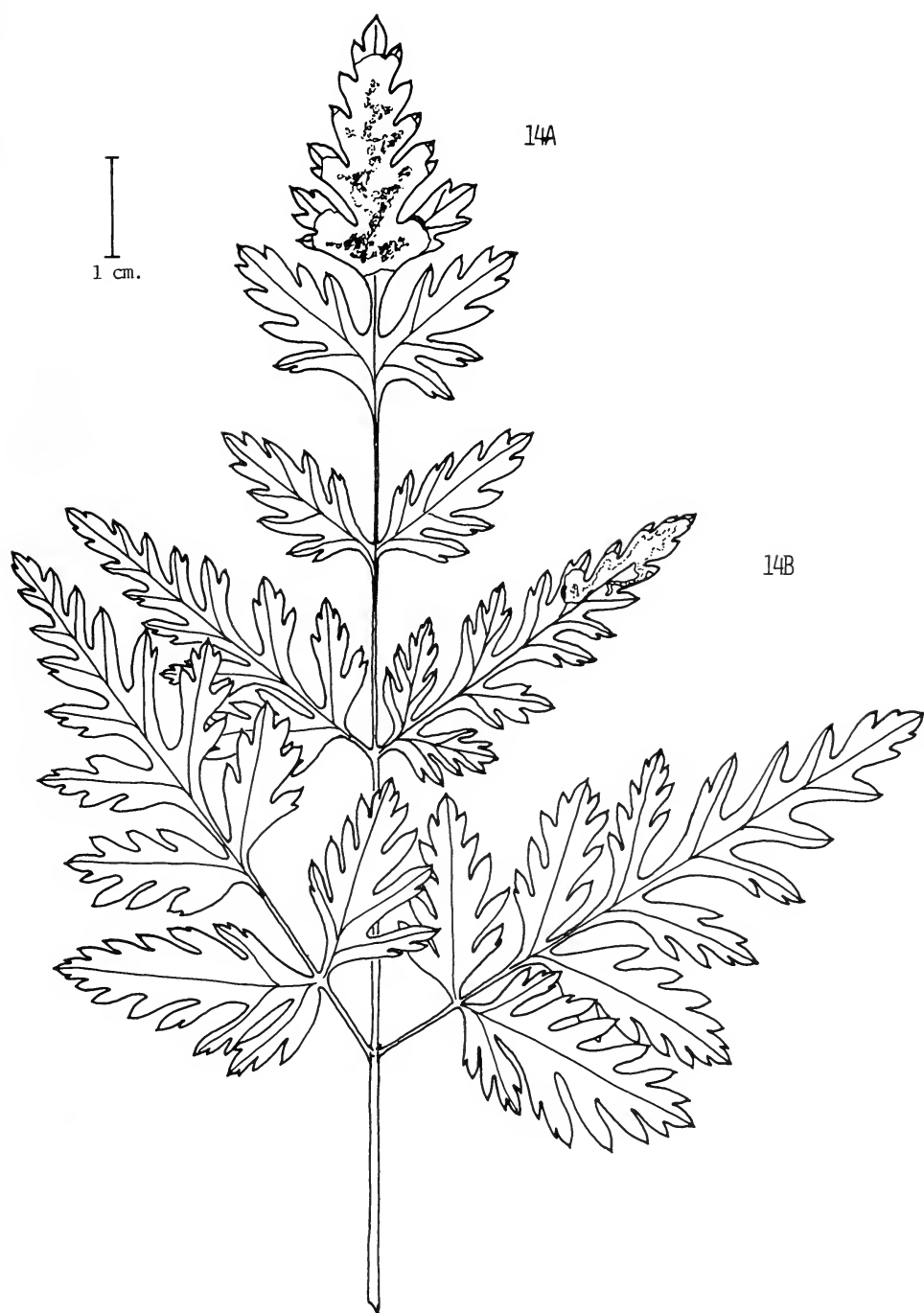


Fig. 14. Leaf of *Conioselinum chinense* (L.) with mines of *Phytomyza* sp. (compare *angelicae* Kalt.) (A) and *P. sitchensis* n. sp. (B).





SOLITARY WASPS FROM SUBARCTIC NORTH AMERICA –  
II. SPHECIDAE FROM THE YUKON AND NORTHWEST  
TERRITORIES, CANADA: DISTRIBUTION AND ECOLOGY

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*Quaestiones entomologicae*

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*Sphecid wasps of 35 species were collected in the Yukon and Northwest Territories during the summers of 1967 and 1968. Literature about these species is reviewed. Latitude, vegetation, soil type and slope of the study areas are analyzed as is their use by the wasps, for feeding, preying, nesting and basking. Particularly well represented in these samples are the subfamilies Crabroninae and Pempredoninae, and the genera Ammophila, Podalonia and Tachysphex. Included are circumpolar, Holarctic and Nearctic species. Some of the last-named group range widely, with populations occurring as far south as Florida and Mexico.*

*Trente-cinq espèces de sphégydes ont été récoltées au Yukon et dans les Territoires du Nord-Ouest au cours des étés 1967 et 1968. Le texte comprend un compte-rendu de la bibliographie relative à ces espèces. On y trouvera une analyse de la latitude, de la végétation, de la nature du sol, de la pente des régions étudiées ainsi que de l'utilisation qu'en font les sphégydes en fonction de leur comportement alimentaire et nidificateur, de la sélection des proies et de leur exposition au soleil. Ce sont surtout les sous-familles Crabroninae et Pempredoninae et les genres Ammophila, Podalonia et Tachysphex qui sont bien représentés parmi cette faune. On y trouve aussi des espèces circumpolaires, holarctiques et néarctiques. Pour le dernier groupe nommé, la distribution est très large, avec des populations pouvant atteindre des régions aussi méridionales que la Floride et le Mexique.*

Despite severe climatic conditions and a short season favorable for activity, many species of the family Pompilidae are represented in the subarctic regions of North America (Steiner, 1970). This paper deals with another family of solitary wasps, the Sphecidae, having representatives which were collected in the same study area.

This paper describes habitats and microhabitats, and provides data about the uses made of these by different species of sphecsids. These wasps are much more diversified in their ecological and behavioral characteristics than are pompilids. Sphecsids are well suited for behavior-ecology studies, particularly for those concerning adaptations for avoiding competition at the community level.

#### THE STUDY AREAS

General features and maps of the regions visited and of the localities sampled have been previously presented (Steiner, 1970). Additional data are provided in Table 1.

Climax communities of the boreal forest and taiga do not appear to provide particularly favorable habitats for solitary wasps but some natural or man-disturbed areas in the north are potentially good habitats. These include pits, river banks, lake shores, flats, outwash plains and forest edges. Most of the sphecsids discussed were collected in such places. Figures 1 to 9 illustrate five locality types from which samples were collected.

Table 1. Distribution per species and localities.

Species	N. W. T.															Y. T.												Total number of localities where species found
1. <i>Diploplectron peglowi</i>	I. Ft. Smith (59° 58')	II. Sass River (60° 10')	III. Wood Buffalo (60° 28')	IV. Enterprise (60° 40')	V. Buffalo River (60° 45')	VI. Hay River (60° 45')	VII. Heart Lake (60° 50')	VIII. Kakisa River (61° )	IX. Ft. Providence S. (61° 17')	X. Ft. Providence N. (61° 17')	XI. Birch Lake (62° )	XII. Yellowknife (62° 27')	XIII. Prelude Lake (62° 32')	XIV. Frank Channel (62° 43')	XV. Rae (62° 46')	A. Marsh Lake (60° 30')	B. Pitkhandle Lake (61° 57')	C. Tatchun Lake (62° 20')	D. Minto (62° 37')	E. Stewart River (63° 26')	F. Taylor Creek (63° 30')	G. Mayo (63° 38')	H. Gravel Lake (63° 47')	I. Keno Hill (63° 54')	J. Dawson City (64° 10')			
2. <i>Astata nubecula</i>																												
3. <i>Dryudella picta</i>																												
4. <i>Miscophus americanus</i>																												
5. <i>Tachysphex aethiops</i>																												
6. <i>T. quebecensis</i>																												
7. <i>T. terminatus</i>																												
8. <i>Diodontus</i> sp.																												
9. <i>Mimesa pauper</i>																												
10. <i>Mimamesa clypeata</i>																												
11. <i>M. sp.</i>																												
12. <i>Pemphredon bipartitor</i>																												
13. <i>P. montana</i>																												
14. <i>Ammophila azteca</i>																												



In the Northwest Territories study area, most localities are on plains and plateaus to the west of the Canadian Shield. However, localities XII, XIII and XV are on the Canadian Shield and locality I (Fort Smith) is near its western edge. In this area samples were collected throughout the summers of 1967 and 1968. The Yukon study area was visited only briefly after mid-August of 1968. Locality X (Fort Providence, in the Mackenzie River valley, Fig. 1 and 2) was the most favorable area visited and was the most intensively investigated.

Eleven habitats are recognized. They are characterized below in terms of slope, vegetation and soil. Also described are the uses made of each habitat by its sphecid inhabitants. See Table 2 for an explanation of letters in Figures 1 to 9.

Table 2. Explanation of letters in Figures 1 to 9. (Typical wasp habitat facies and micro-habitats in some Northwest Territories sample localities)

- a = Immature aspen interspersed with willow and shrub
- b = Low spoilbank (small man-made ridge)
- c = Flat area, covered with dense, low vegetation
- d = Patches of *Achillea millefolium* (yarrow)
- e = Flat area, sparsely vegetated
- f = Patches of *Epilobium* species (fireweed)
- g = Spruce/Jackpine forest (interspersed with aspen)
- h = Collapsed cutbanks (steep slope)
- i = Patches of shrubby vegetation (*Rosa* sp., *Salix* sp., *Betula* sp., *Alnus* sp., etc.)
- j = Edge of mature forest (with shrub understory)
- k = Decaying exposed tree roots and branches
- l = Decaying, partially buried logs
- m = Spruce forest
- n = Tall grasses
- o = Vegetated spoilbank (gentle slope)
- p = Vegetated ditchside
- q = Non-vegetated man-made disturbed area
- r = Edge of mature forest
- s = Hummocky, richly vegetated area
- t = Poorly drained flat bottom of shallow borrow pit
- u = Elevated area left around base of large tree
- v = Tension zone (ecotone); transition zone from bog to upland (dense low shrubby vegetation)
- w = Cutbank of borrow pits resulting from excavation
- x = Spoilbank in the process of becoming vegetated
- y = Flat vegetated flood plain of river

1). *Recently disturbed, flat, unvegetated areas with friable (often sandy) soil* (q, Fig. 5 and 7). — These areas border the highway in dugouts, borrow pits, sand and gravel pits (Fig. 5), or border lake shores (Fig. 7) and river banks and were in localities I, VI, VII, XI, XII, XIII and XIV.

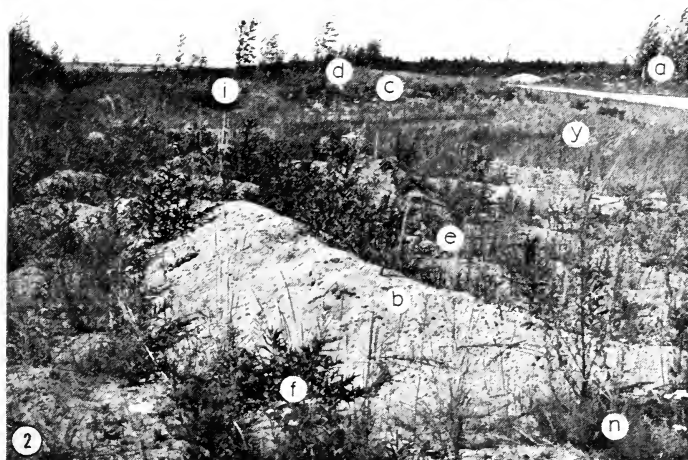


Fig. 1-2. Flood plain of Mackenzie River with flat, low vegetated areas (Fig. 2) and juxtaposition of spoilbanks and forest edge habitats, of sandy soil (Fig. 1). (Ft. Providence: X, 9 August 1967). Fig. 3. Shallow borrow pit along highway, in the process of becoming vegetated; friable soil. (Frank Channel: XIV, 8 August 1967)

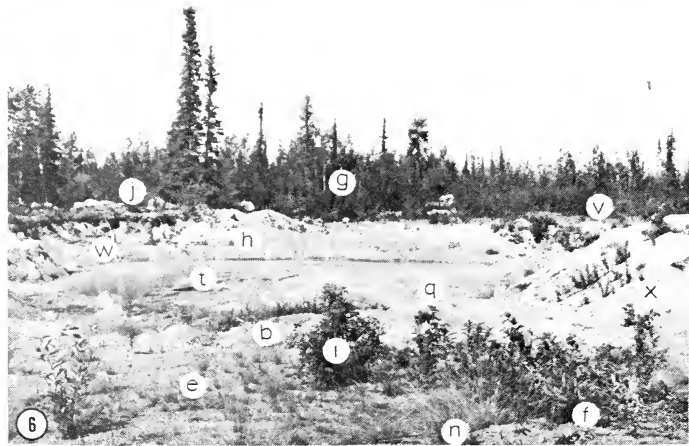


Fig. 4-5. Man-made gravel/sand pit, along highway, with friable soil: general view (Fig. 5) and detail of gently sloping area (Fig. 4) with various microhabitats. (Birch Lake: XI, 2 August 1967). Fig. 6. Deep borrow pit in compact, poorly drained soil, with tension zone between bog and upland. (Rae: XV, 8 August 1967)

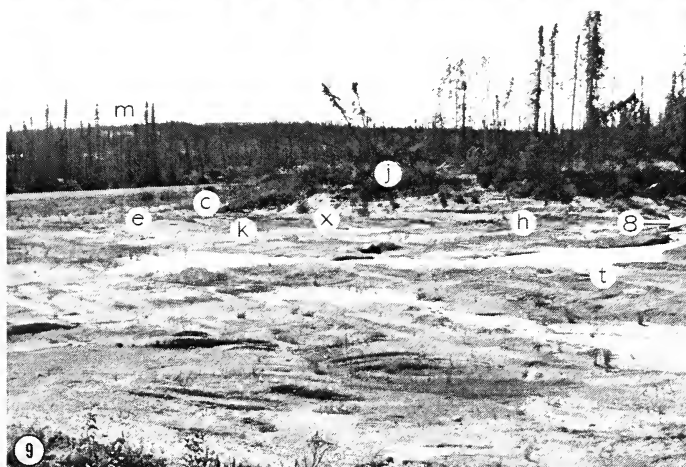
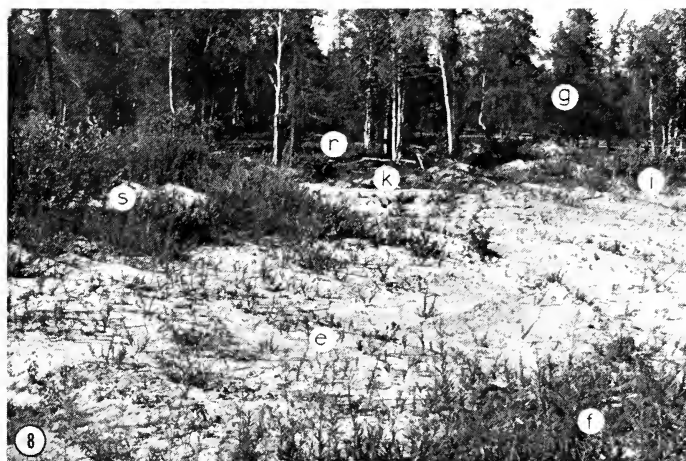


Fig. 7-9. Disturbed areas on sandy lake shore areas (Fig. 7-8) near forest edges, and extensive man-made bare and poorly drained area, along the highway (Fig. 9). (Prelude Lake: XIII, 7 August 1967)

If it is situated adjacent to a vegetated area this habitat is used occasionally by wasps for basking early in the morning. Those most frequently observed were members of *Astata nubecula*, members of the genera *Ammophila*, *Podalonia* and *Tachysphex* and a few pompilids and crabronines. A few females of *Tachysphex terminatus* were seen digging in such areas, but usually in sparsely vegetated areas.

2). *Recently disturbed, sloping, unvegetated areas of friable soil* (*h*, Fig. 5 and 9). — These often consist of steep (*h*, Fig. 5) or gently sloping, man-made, collapsed cutbanks and spoilbanks and were found in localities I, VII, XI (Fig. 5, *h*), XII, and XIII (Fig. 9, *h*).

Such areas resemble habitat type 1 but, when favorably exposed to the morning sun, are used more consistently by wasps for basking. Males of *Astata nubecula* were at site *h* (Fig. 5) perched on prominent features of the landscape such as boulders and stumps that were also used as observation posts. Specimens representing the other taxa listed for habitat 1 were found in habitat 2, also.

3). *Man-made, poorly-drained, flat bottoms of borrow pits, usually in compact soil* (*t*, Fig. 6 and 9). — This habitat was extensive in locality XIII (*t*, Fig. 9), less so in locality XV (*t*, Fig. 6).

A relatively large amount of soil moisture rendered this type of habitat generally unsuitable for wasps, although a few females of *Ammophila* and *Podalonia* carried prey across such areas. Drier sections of this habitat were used for nesting by a few females of some species, such as *Cerceris nigrescens* (XV, Fig. 6), which usually nest in habitats with more friable soil (XI, Fig. 4 and 5).

4). *Flat or gently sloping, sparsely-vegetated areas* (*e* in most Figures, *y* in Fig. 2). — Usually of friable soil, these areas are: (a) man-made, occurring in pits (Fig. 4 and 5); or (b) natural, on flood plains of rivers (*y*, Fig. 2) and lake shores. They were extensively represented in most localities, particularly along flood plains of the Mackenzie (IX and X) and of the Hay Rivers (VI), and shores of Great Slave Lake (XIV) and Prelude Lake (XIII).

These areas were used extensively as nesting grounds by females of *Ammophila*, *Podalonia*, *Tachysphex* (particularly *T. aethiops*, the most common species of this genus), *Nysson*, *Cerceris* and some Crabroninae. A few nests of *Oxybelus* were seen here, but they were more common on more sloping ground. Females of small species of Pemphredoninae and Crabroninae, which prey on small insects, used these areas mainly for hunting and less frequently for basking and feeding. Females of the larger wasp species hunted mainly in more densely vegetated areas, which had a more abundant flora and insect fauna.

5). *Flat areas, densely covered with herbaceous vegetation* (*c* in most Figures). — Most localities included this type of habitat, but it was best developed along the Mackenzie River (X, Fig. 1 and 2).

An abundant and diverse insect fauna was found in these areas, including acridoid grasshoppers, leafhoppers, small beetles, many flies, bugs, lepidopterous caterpillars, and representatives of other groups. Most flowers on which the sphecids wasps fed occurred in these areas.

Although many wasps hunted and fed in this type of habitat, nests were rare. Sphecids of the genus *Tachysphex* and pompilids used this habitat most intensively as hunting ground. Females of *Tachysphex* prey mainly on the immature acridids and tetrigids, abundant in these places. Other hunters observed were females of *Ammophila* and *Podalonia* species.

Patches of fireweed (*Epilobium*, *f*, Fig. 1, 2, 4 and 8), yarrow (*Achillea millefolium*, *d*, Fig. 1 and 2), and undetermined umbellifers, common in this habitat, were intensively exploited as a source of food by wasps of many species, particularly in the morning.

6). *Low spoilbanks and man-made ridges of friable soil in the process of becoming vegetated* (*b*, Fig. 1 and 2; *o*, Fig. 4; *x*, Fig. 5, 6 and 9). — This type of habitat provides nesting



grounds for many species. Along the Mackenzie River (X, Fig. 1 and 2) these areas were used as nesting grounds by females of *Oxybelus uniglumis quadrinotatus*, *Mimesa pauper*, *Mimesa clypeata*, *Dryudella picta* and *Diploplectron peglowi*. *Dryudella* males exhibited territorial behavior, as described for *Astata nubecula* (Evans, 1970: 487-488). The only specimens of *Miscophus americanus* from the study areas were found in a similar habitat (locality XI).

These areas were used extensively by female insects which prey on sphecids: the inquiline sphecids of the genus *Nysson*; chrysidid wasps; and parasitoid Diptera. Other sphecids did not extensively use these areas as hunting grounds.

Patches of yarrow (*d*, Fig. 1) and fireweed (*f*, Fig. 2) growing in these areas were exploited for food by many wasps. Basking was observed on the spoilbanks. On spoilbanks situated adjacent to shrubby and sparsely-forested habitats (*a*, Fig. 1), interactions between and within species were most intense, frequent and complex due to the addition of Pemphredoninae and Crabroninae, characteristic of shrubby habitats.

7). *Shrubby, brushy and sparsely-forested areas, with understory* (*a*, *i*, *j*, *r*, *s*, *v*, Fig. 1-9). — Such habitat includes stands of aspen interspersed with willow and shrub (*a*, Fig. 1), edges of mature forest with shrub understory (*j*, Fig. 3, 5 and 9; *r*, Fig. 7) and ecotones (tension zones) such as those between bog and upland, having dense, low, shrubby vegetation (*v*, Fig. 6).

These areas provide both nesting and hunting sites for those pemphredonines and crabronines that are twig nesters, such as *Mimesa* sp. and *Pemphredon bipartitor* for the former, *Ectemnius* for the latter. But they provide only hunting sites for those crabronines that are ground nesters, such as *Crabro latipes*. An occasional nest of *Tachysphex aethiops* and of *Podalonia robusta* was found on the ground, but only in thinly-vegetated areas or at the edges of this habitat type. Females of *Crabro latipes* and *Ectemnius nigrifrons* hunted in the leaves of shrubs. Females of the philanthine *Cerceris nigrescens nigrescens*, which prey on small weevils (Evans, 1970: 501; Muesebeck et al., 1951: 1009; Scullen and Wold, 1969: 212), used extensively as hunting grounds area *v* (Fig. 6).

Males of crabronines, especially *C. latipes*, were numerous and were probably attracted by the hunting females. They attempted to mate with females and with other males particularly at sites *a* (Fig. 1) and *j* (Fig. 9). Males of some undetermined pemphredonines behaved similarly. A few males of the larrine *Tachysphex aethiops* were also found in such a habitat, investigating the leaves of a small *Alnus* bush. They were perhaps feeding, as individuals of several other species of Larrinae are known to lick exudations of sap from various plants or shrubs.

Between bouts of hunting, the occasional crabronine basked in this habitat, flattening itself on an exposed leaf or against a tree trunk. Early in the morning, however, they basked mainly on boulders or on the ground in non-vegetated or sparsely-vegetated areas adjacent to the brushy hunting grounds.

8.) *Patches of shrubby vegetation (including populations of Rosa, Salix, Betula and Alnus)* (*i*, Fig. 4 and 5) or *hummocky, richly-vegetated areas* (*s*, Fig. 8). — These areas provide suitable situations for the twig-nesting species. They were also visited by ground-nesting crabronines and pemphredonines during their hunting trips. The few specimens seen or captured of *Lestiphorus cockerelli*, *Gorytes albosignatus* and *Alysson triangulifer* were found in this habitat. From circumstantial evidence, I think the latter were hunting, not nesting, here. One individual of *G. albosignatus* was found digging the soil in a different habitat (site *b*, Fig. 2), and insofar as is known Nearctic *Alysson* females nest in the soil (Muesebeck et al., 1951: 980).

9). *Decaying, often partially buried logs (l, Fig. 4) and decaying exposed tree roots and branches (k, Fig. 5 and 8).* — These sites were visited by pemphredonines and crabronines some of which inspected abandoned galleries of wood borers (hunting or nest-seeking behavior?). Female crabronines of *Ectemnius arcuatus* and *E. dives* are known to nest in logs, timber and stems (Muesebeck et al., 1951: 1026-1027). A few wasps (pemphredonines, crabronines, *Ammophila azteca* and others) basked in these places, and males of *Astata nubecula* used them for observation posts.

10). *Vertical banks (sand cliffs; cutbanks; river cutbanks; cutbanks of borrow pits) (w, Fig. 6).* — In locality VI, females of the small pemphredonine *Diodontus* were found inspecting, both in flight and by walking, such cutbanks and the burrows therein, possibly for prey or for nesting sites. Other wasps found here consistently were: a small crabronine, undetermined, possibly a member of the genus *Crossocerus*; some vespids; and some chrysidids. Occasional basking was also observed here.

11). *Dense, spruce-jackpine (g, Fig. 3, 5, 6, 7 and 8) and spruce stands (m, Fig. 4 and 9).* — These areas were seldom visited by wasps.

*Discussion.* — When nesting, hunting, feeding and basking sites were close together, as in locality X (Fig. 1), conditions appeared particularly favorable for many wasps. Indeed, the speed with which prey capture and nest provisioning can be completed may be crucial, particularly in northern climates where favorable weather is limited (Evans, 1970).

Considerable segregation in habitat and microhabitat was noticed among sphecids wasps, much more so than among the spider wasps studied previously (Steiner, 1970). Competition among species is thus considerably reduced, and is further reduced by behavioral specialization in prey selection and hunting techniques (Evans, 1970). Further segregation is achieved by some stratification of the nest cells in the soil, at different depths according to species (Evans, 1970). However, there was little species segregation at feeding and at basking sites.

## ANNOTATED LIST OF SPECIES

### Family Sphecidae

#### Subfamily Astatinae

#### Genus *Diploplectron* Fox

*Known biology.* — Females nest in open sandy places (Evans, 1957: 180). Prey consists of adults or nymphs of Hemiptera. Williams (1946: 648) provides details.

*Known distribution.* — North America and South Africa (Evans, 1957: 180).

#### 1. *Diploplectron peglowi* Krombein.

*Known distribution.* — New York: Oswego Co. (Muesebeck et al., 1951: 939).

*Author's records.* — NORTHWEST TERRITORIES. — X, ♂, 2 ♀♀ 31 July 1967. XIII, 2 ♂♂, ♀ 6 August 1967 (♀ hunting); ♂ 7 August 1967.

#### Genus *Astata* Latreille

*Known biology.* — Females of this genus provision their nests with Hemiptera, especially pentatomids and lygaeids (Muesebeck et al., 1951: 939).

#### 2. *Astata nubecula* Cresson.

*Known biology.* — Females nest in bare, hard, stony soil, and provision their nests with immature stink bugs (*Chlorochroa uhleri* Ståhl) carried in flight (Evans, 1970). Nymphs

of *Thyanta* have also been recorded as prey (Krombein et al., 1967: 387). Males exhibit territorial behavior (Evans, 1970).

*Known distribution.* — Western United States, Oregon to New Mexico north to Idaho (Muesebeck et al., 1951: 940). Wyoming: Jackson Hole (Evans, 1970). Alberta (Strickland, 1947: 129).

*Author's records.* — NORTHWEST TERRITORIES. — VIII, ♂ 10 August 1967 (returns and lands on exactly the same spot); ♀ 2 August 1967 (exploring). XIII, 3 ♂♂ 30 July 1968 (each lands on conspicuous, elevated objects such as stumps, fallen logs and rocks); 2 ♂♂, ♀ 7 August 1967. XIV, ♂ 8 August 1967 (returns and lands on same spot).

Genus *Dryudella* Spinola

3. *Dryudella picta* (Kohl).

*Author's records.* — NORTHWEST TERRITORIES. — X, ♂, ♀ 17 July 1968 (*in copula*, the male carrying the female under him in flight in prey-like fashion, and landing from time to time); ♂ 21 July 1967 (basking in the morning sun). XIII, 2 ♂♂ 7 August 1967 (returning to and landing on same spots, repeatedly).

Subfamily Larrinae  
Tribe Miscophini  
Genus *Miscophus* Jurine

*Known biology.* — Females nest in sandy soil and provision their nest cells with tiny spiders transported in a series of low flights (Kurczewski, 1969).

4. *Miscophus americanus* (W. Fox).

*Known biology.* — Kurczewski (1969) presented a detailed study of the biology of this species. Notes were published by Hartman (1905: 69-70), and Krombein (1952b: 328). Adults are found on sand, on bare places and in woods. Females nest in well-packed sand in slightly sloping areas. Prey consists of immature spiders of the families Epeiridae (Hartman, 1905) and Theridiidae (Kurczewski, 1969). The latter author provides data on prey hunting behavior, nest provisioning, nest structure, and position of the egg on the prey.

*Known distribution.* — Eastern North America, from New York south to Florida and west to Colorado (Muesebeck et al., 1951: 944) and Alberta (Strickland, 1947: 129).

*Author's records.* — NORTHWEST TERRITORIES. — XI, 2 ♂♂ 2 August 1967.

Tribe Tachytini  
Genus *Tachysphex* Kohl

*Known biology.* — Prey species are orthopteroids, mostly immature acridids, but females of some species also capture mantids and blattids (Muesebeck et al., 1951: 950).

5. *Tachysphex aethiops* (Cresson).

*Known biology.* — A nest was found on flat, friable sand 2 meters from a river bank. The prey therein was an immature acridid grasshopper of the genus *Trimerotropis* (Evans, 1970: 489-490).

*Known distribution.* — Western United States in mountains (Muesebeck et al., 1951: 950). Wyoming: Jackson Hole (Evans, 1970).

*Author's records.* — NORTHWEST TERRITORIES. — VI, ♂, ♀ 29 July 1967; ♂ 12

August 1967. X, ♀ 11 August 1968 (apparently hunting); ♀ 25 August 1967. XII, 3 ♀♀ 29 July 1968 (hunting and nest digging in sandy hillocks). XIII, 2 ♂♂, 2 ♀♀ (former investigating leaves of small *Alnus* bush) 30 July 1968; ♀ 6 August 1967. XIV, 2 ♂♂ 8 August 1967.

6. *Tachysphex quebecensis* Provancher.

*Known biology.* — Prey: immature acridids of the genera *Camnula* and *Melanoplus* (Krombein et al., 1967: 393).

*Known distribution.* — Transcontinental in northern United States and southern Canada, Quebec to California, in north (Krombein et al., 1967: 393; Muesebeck et al., 1951: 952).

*Author's records.* — NORTHWEST TERRITORIES. — X, ♂ 25 July 1967; ♀ 26 July 1967. XII, ♀ 29 July 1968. XIV, ♂, ♀ 26 July 1968.

7. *Tachysphex terminatus* (F. Smith)

*Known biology.* — Adults are found in woods and in barrens (Krombein et al., 1952b: 330). Nests are in open places, in sand or in loose topsoil (Krombein et al., 1958: 188; Muesebeck et al., 1951: 953). Prey includes tetrigids and immature acridids of many genera (Muesebeck et al., 1951: 953). The latter group includes *Melanoplus* and *Tryxalus* (Krombein et al., 1958: 188; Kurczewski, 1966a), and *Chorthippus curtippennis* (Harris) (Evans, 1970: 491). Female closes entrance while away from burrow (Evans, 1970). Male behavior was studied by Kurczewski (1966b). Data about population ecology of this species are recorded by Kurczewski and Harris (1968).

*Known distribution.* — Transcontinental, in the north from Quebec to British Columbia; southward in the east to Georgia and westward to Arizona (Krombein et al., 1967: 393; Muesebeck et al., 1951: 953). Alberta (Strickland, 1947: 129).

*Author's records.* — NORTHWEST TERRITORIES. — XIII, ♀ 30 July 1968 (starting nest digging in the ground). XIV, 2 ♂♂ 8 August 1967.

Subfamily Pemphredoninae

Tribe Psenini

Genus *Diodontus* Curtis

*Known biology.* — Nests are in cavities in logs, or stems of plants, such as canes of *Rubus* (Muesebeck et al., 1951: 958; Spooner, 1948: 129-172). Females of Palearctic species prey on aphids and psyllids, which are carried ventrally by the middle legs (Spooner, 1948). Prey records are not available for the Nearctic species.

8. *Diodontus* sp. (or spp.?).

*Author's records.* — NORTHWEST TERRITORIES. — III, ♀ 14 August 1967. VI, 3 ♂♂, 2 ♀♀, 29 July 1967 (investigating vertical cutbanks); ♂, ♀ 12 August 1967.

Genus *Mimesa* Shuckard

Subgenus *Mimesa* (*sensu stricto*)

*Known biology.* — Females nest in soil. Prey consists of cicadellids, which the female carries with her middle legs (Muesebeck et al., 1951: 958; Spooner, 1948).

9. *Mimesa pauper* Packard.

*Known biology.* — Adults at edge of woods on high foliage (Kurczewski and Kurczew-

ski, 1963:146).

*Known distribution.* — Transition zone east of Rocky Mountains (Muesebeck et al., 1951: 960).

*Author's records.* — NORTHWEST TERRITORIES. — X, ♀ 11 July 1968 (investigating insect burrows, holes, in the soil); 3 ♀♀ 31 July 1967 (same remark). XII, one (sex?) 29 July 1968 (same remark). XIII, 4 ♂♂ (on leaves of small trees) 7 August 1967. XIV, ♂ 26 July 1968; 4 ♀♀ 8 August 1967.

#### Subgenus *Mimumesa* Malloch

*Known biology.* — Females of Palaearctic species nest in cavities in logs and stems. Their prey consists of delphacids and cicadellids, which the female wasp carries in her mandibles (Spooners, 1948). Data about biology are not available for Nearctic species.

#### 10. *Mimesa clypeata* (W. Fox).

*Known distribution.* — Western North America: California and Nevada north to Alaska (Muesebeck et al., 1951: 961).

*Author's records.* — NORTHWEST TERRITORIES. — IX, ♀ 1 August 1967 (investigating the ground, holes, burrows). X, ♀ 26 July 1967.

#### 11. *Mimesa* species.

*Author's records.* — NORTHWEST TERRITORIES. — X, ♀ 22 July 1967 (flying around shrubs). XII, ♂ 4 August 1967. XIV, 2 ♀♀ 8 August 1967 (flying around young aspen and big boulders).

#### Tribe Pemphredonini

#### Genus *Pemphredon* Latreille

*Known biology.* — Females nest in twigs, deserted galls, abandoned beetle burrows, or in rotten wood, and provision the cells with bugs of the family Aphidae (Muesebeck et al., 1951: 965).

#### 12. *Pemphredon bipartitor* W. Fox.

*Known biology.* — Nests in twigs of sumac and elder. Prey: ?*Eriosoma lanigerum* (Hausmann); *Rhopalosiphum rhois* Monell (Muesebeck et al., 1951: 966).

*Known distribution.* — Eastern United States, New York to Texas (Muesebeck et al., 1951: 966).

*Author's records.* — NORTHWEST TERRITORIES. — XIII, 2 ♂♂ 7 August 1967.

#### 13. *Pemphredon montana* Dahlbom.

*Known distribution.* — Holarctic. Nearctic Region: British Columbia. Palaearctic Region: Europe (Muesebeck et al., 1951: 965).

*Author's records.* — NORTHWEST TERRITORIES. — VII, ♀ mid-July 1968.

#### Subfamily Sphecinae

#### Tribe Ammophilini

#### Genus *Ammophila* Kirby

#### 14. *Ammophila azteca* Cameron.

*Known biology.* — Females prey on small larvae of sawflies and moths (recorded families — Geometridae, Gelechiidae, Sphingidae) and carry the prey in flight (Evans, 1970: 485). Evans (1965) presented a detailed study of the biology of this species.

*Known distribution.* — Wyoming: Jackson Hole (Evans, 1970).

*Author's records.* — NORTHWEST TERRITORIES. — III, ♂ 14 August 1967. V, ♀ 14 August 1967. VI, ♀ 29 July 1967; ♀ 12 August 1967. VII, ♀ 11 August 1967. IX, ♂ 1 August 1967. X, ♀ 11 July 1968; ♂, ♀ 17 July 1968; 3 ♂♂, ♀ 22 July 1967 (feeding on *Achillea* sp.); ♀ 25 July 1967; ♂, ♀ (*in copula*) 26 July 1967. XI, ♂, ♀ 2 August 1967; ♀ 8 August 1967. XII, ♂ 7 August 1967. XIII, 3 ♂♂, 2 ♀♀ 6 August 1967; ♀ 7 August 1967. XIV, ♂ 26 July 1968; ♂, ♀ 8 August 1967. XV, ♀ 8 August 1967. YUKON TERRITORY. — B, ♀ 15 August 1968. E, 3 ♀♀ 10 August 1968. G, 3 ♀♀ 12 August 1968.

15. *Ammophila mediata* Cresson.

*Known distribution.* — Ontario to British Columbia, Michigan to Colorado (Muesebeck et al., 1951: 976). Wyoming: Jackson Hole (Evans, 1970). Alberta (Strickland, 1947: 129).

*Author's records.* — NORTHWEST TERRITORIES. — I, 2 ♀♀ 15 August 1967. IV, ♀ 28 July 1967. X, ♂, ♀ 21 July 1967. XIII, ♀ 30 July 1968. XIV, ♂ 26 July 1968; ♀ 8 August 1967. YUKON TERRITORY. — B, ♀ 15 August 1968. C, ♀ 9 August 1968.

16. *Ammophila strenua* Cresson.

*Known distribution.* — Western United States (Muesebeck et al., 1951: 977). Wyoming: Jackson Hole (Evans, 1970).

*Author's records.* — NORTHWEST TERRITORIES. — X, ♂ 21 July 1967.

Genus *Podalonia* Spinola

17. *Podalonia luctuosa* (F. Smith).

*Known distribution.* — Canada, United States — western and northern tier of states to Maine (Muesebeck et al., 1951: 977). Wyoming: Jackson Hole (Evans, 1970). Alberta (Strickland, 1947: 128).

*Author's records.* — NORTHWEST TERRITORIES. — II, ♂ 14 August 1967. III, ♂ 14 August 1967. YUKON TERRITORY. — McGregor Creek, ♂ 10 August 1968.

18. *Podalonia robusta* (Cr.)

*Known biology.* — Prey: noctuid larva (Krombein et al., 1967: 404; *see also* Evans, 1963: 237).

*Known distribution.* — Canada; United States — western and northern tier of states to Maine (Muesebeck et al., 1951: 978). Alberta (Strickland, 1947: 128).

*Author's records.* — NORTHWEST TERRITORIES. — VI, ♀ 29 July 1967. IX, ♂ 1 August 1967. X, 6 ♂♂, ♀ 11 July 1968; ♀ 17 July 1968; ♂, ♀ 22 July 1967; 3 ♀♀ 25 July 1967; ♂, ♀ (*in copula*), ♀ 31 July 1967. XII, ♂, ♀ 29 July 1968; ♂ 7 August 1967. XIV, ♀ 8 August 1968. YUKON TERRITORY. — B, 2 ♀♀ (feeding on flowers and hunting(?) on the ground, respectively) 15 August 1968.

Also seen (but not captured): an entirely black specimen of (?) *Podalonia* sp. (XII).

Subfamily Nyssoninae  
Tribe Alyssonini  
Genus *Alysson* Panzer

19. *Alysson triangulifer* Provancher.

*Author's records.* — NORTHWEST TERRITORIES. — IX, ♀ 1 August 1967 (investigating leaves, in shrubs).

Tribe Nyssonini  
Genus *Nysson* Latreille

*Known biology.* — Larvae of this genus are inquiline in the nests of other sphecids wasps and bees (Muesebeck et al., 1951).

20. *Nysson lateralis* Packard.

*Known distribution.* — Chiefly Transition zone east of Rockies (Muesebeck et al., 1951: 983).

*Author's records.* — NORTHWEST TERRITORIES. — VII, ♀ 11 August 1967. IX, 2 ♀♀ 1 August 1967. X, ♀ 26 July 1967. XI, 2 ♀♀ 8 August 1967. XIII, ♀ 6 August 1967.

21. *Nysson subtilis* W. Fox.

*Known biology.* — Adults found along trail in open areas (Krombein, 1952a: 181).

*Known distribution.* — Pennsylvania, Illinois (Muesebeck et al., 1951: 983).

*Author's records.* — NORTHWEST TERRITORIES. — X, ♀ 22 July 1967; ♀ 25 July 1967; ♂, ♀ 31 July 1967. XI, ♀ 2 August 1967.

Tribe Gorytini  
Genus *Lestiphorus* Lepeletier

22. *Lestiphorus cockerelli* (Rohwer).

*Known distribution.* — Eastern United States, northern tier west to Colorado (Muesebeck et al., 1951: 988).

*Author's records.* — NORTHWEST TERRITORIES. — X, ♀ 31 July 1967.

Genus *Gorytes* Latreille

23. *Gorytes albosignatus* W. Fox.

*Known distribution.* — Western United States, North Dakota to Montana, south to Nebraska (Muesebeck et al., 1951: 991). Wyoming: Jackson Hole (Evans, 1970: 494). Alberta (Strickland, 1947: 126).

*Author's records.* — NORTHWEST TERRITORIES. — X, ♀ 17 July 1968 (digging in sand hill).

Subfamily Philanthinae  
Tribe Cercerini  
Genus *Cerceris* Latreille

24. *Cerceris nigrescens nigrescens* F. Smith.

*Known biology.* — Females nest in the ground, and prey on weevils of the following

taxa: *Hyperodes delumbis* (Gyllenhal); *Sitona hispidula* (Fabricius); *Gymnaetron* sp.; *Gymnaetron antirrhini* (Paykull) (Evans, 1970: 501; Muesebeck et al., 1951: 1009; Scullen and Wold, 1969: 212). Scullen (1965: 494-495) lists the names of the plant species visited by adults of *C. nigrescens*.

*Known distribution.* — This is the most widely distributed species of *Cerceris* in North America, ranging from New England and adjacent southeastern Canada westward to the Pacific coast, northward to Alaska and south to Nevada and North Carolina (Muesebeck et al., 1951: 1009; Scullen, 1965: 492; Scullen and Wold, 1969: 212). Alberta (Strickland, 1947: 130).

*Author's records.* — NORTHWEST TERRITORIES. — I, ♀ 15 August 1967. VII, 2 ♀♀ 11 August 1967. IX, ♂, ♀ 1 August 1967. X, ♂ 11 July 1968; 3 ♂♂, 2 ♀♀ 22 July 1967; ♂, ♀ 25 July 1967; ♀ 31 July 1967. XI, 3 ♀♀ 2 August 1967; ♀ 8 August 1967. XII, ♂ 4 August 1967. XIII, ♀ 30 July 1968; ♀ 6 August 1967. XIV, ♂ 26 July 1968; 2 ♀♀ 8 August 1967. YUKON TERRITORY. — E, ♂, 3 ♀♀ 10 August 1968.

#### Subfamily Crabroninae

##### Tribe Crabronini

##### Genus *Crabro* Fabricius

*Known biology.* — Females nest principally in soil, though occasionally in rotten wood and prey on flies (Muesebeck et al., 1951: 1015). Kurczewski and Acciavatti (1968) review nesting behavior of the Nearctic species.

#### 25. *Crabro latipes* F. Smith.

*Known biology.* — A detailed study of nesting behavior is provided by Kurczewski, Burdick and Gaumer (1969). Nests are in open areas with sparse vegetation. Prey consists of a wide variety of average-size flies of rather stocky build, such as individuals of *Musca domestica* Linnaeus (Muesebeck et al., 1951: 1017) and *Musca autumnalis* DeGeer (Kurczewski and Harris, 1968).

*Known distribution.* — Transcontinental in the north, in Canada, Alaska and the Canadian and Transition zones of conterminous United States (Muesebeck et al., 1951: 1017). Alberta (Strickland, 1947: 127).

*Author's records.* — NORTHWEST TERRITORIES. — VI, ♂, 4 ♀♀ 29 July 1967. VII, ♂ 11 August 1967. X, ♂, ♀ 11 July 1968; ♂ 17 July 1968 (on leaves of willows? pouncing on other males of apparently the same species); ♀ 21 July 1967 (investigating holes in the ground); ♀ 22 July 1967; ♀ 25 July 1967; ♂ 26 July 1967; 2 ♂♂, ♀ 31 July 1967. XI, 3 ♂♂ 2 August 1967. XII, ♀ 7 August 1967 (on leaves, shrub). XIII, ♂ 6 August 1967 (on leaves, shrub); 4 ♂♂ 7 August 1967. XIV, 2 ♂♂ 8 August 1967 (on leaves of small *Alnus* ?). YUKON TERRITORY. — G, ♂ 12 August 1968.

#### 26. *Crabro* sp.

*Author's records.* — NORTHWEST TERRITORIES. — XIII, ♀ 30 July 1968.

#### Genus *Crossocerus* Lepeletier and Brullé

*Known biology.* — Females usually nest in soil, occasionally in cracks in walls or in abandoned beetle burrows in wood. Prey consists of small flies (Muesebeck et al., 1951: 1020).

#### 27. *Crossocerus* species.



*Author's records.* — NORTHWEST TERRITORIES. — IX, 31 July 1967. X, ♂, 3 ♀♀ 31 July 1967. XIV, ♀ 8 August 1967.

Genus *Ectemnius* Dahlbom

28. *Ectemnius arcuatus* Say.

*Known biology.* — Females nest in logs. They prey on flies of the species *Musca domestica* L. (Muesebeck et al., 1951: 1026; under the name *Hypocrabro chrysargirus* (Lepeletier and Brullé)).

*Known distribution.* — Transcontinental in Transition and Austral zones (Muesebeck et al., 1951: 1026; under the name *Hypocrabro chrysargirus* (Lepeletier and Brullé)).

*Author's records.* — NORTHWEST TERRITORIES. — X, ♀ 17 July 1968 (feeding on *Epilobium* sp. flowers).

29. *Ectemnius dives* (Lepeletier and Brullé).

*Known biology.* — Females nest in logs, timber and stems. Prey consists of muscoid Diptera (Muesebeck et al., 1951: 1027). Kurczewski and Kurczewski (1963: 148) observed males on flowers of *Daucus carota* and *Achillea millefolium*.

*Known distribution.* — Holarctic. Nearctic Region: transcontinental in Canadian and Transition zones of Canada and United States (Muesebeck et al., 1951: 1027). Alberta (Strickland, 1947: 127). Palaearctic Region: Germany, Austria, Switzerland and Morocco (Leclercq, 1949: 11).

*Author's records.* — NORTHWEST TERRITORIES. — X, 2 ♂♂ 11 July 1968; ♂ 25 July 1967; 2 ♂♂ 26 July 1967; 3 ♀♀ 31 July 1967.

30. *Ectemnius lapidarius* (Panzer).

*Known biology.* — Adults are in open woods and at the edge of woods, on flowers of *Solidago* sp., and of *Daucus carota* (Kurczewski and Kurczewski, 1963: 148).

*Known distribution.* — Holarctic. Nearctic Region: Pennsylvania (Kurczewski and Kurczewski, 1963: 148). Wyoming: Jackson Hole (Evans, 1970: 492). Alberta (Strickland, 1947: 127). Palaearctic Region: Finland, Germany and Austria (Leclercq, 1949).

*Author's records.* — YUKON TERRITORY. — Lake Labarge, ♀ 6 August 1968. G, ♀ 12 August 1968.

31. *Ectemnius nigrifrons* (Cresson).

*Known biology.* — Recorded as prey is the fly species *Syrphus ribesii* (Linnaeus) by Muesebeck et al., (1951: 1024; under the name *Clytochrysus nigrifrons*).

*Known distribution.* — Holarctic. Nearctic Region: transcontinental, chiefly in Transition zone (Muesebeck et al., 1951: 1024; under the name *Clytochrysus nigrifrons*). Alberta (Strickland, 1947: 127). Palaearctic Region: Switzerland (Leclercq, 1949).

*Author's records.* — NORTHWEST TERRITORIES. — II, ♀ 14 August 1967. V, ♀ 14 August 1967. IX, ♂, 2 ♀♀ 1 August 1967. X, ♀ 11 July 1968; 2 ♂♂ 17 July 1968. XIII, ♀ 7 August 1967. YUKON TERRITORY. — C, 2 ♀♀ 9 August 1968 (stalking behavior: react to slightest movements by orienting responses; also intense visual scanning; hunting behavior?); 2 ♀♀ 10 August 1968 (same remark, concerning hunting behavior?). E, ♀ 10 August 1968. G, 2 ♀♀ 12 August 1968.

32. *Ectemnius trifasciatus* (Say).

*Known distribution.* — Transition zone of Canada and United States, east of the

Cascade and Sierra Nevada ranges (Leclercq, 1949: 11; Muesebeck et al., 1951: 1027, under the name *Hypocrabro trifasciatus*). Alberta (Strickland, 1947: 127).

*Author's records.* — NORTHWEST TERRITORIES. — III, ♀ 14 August 1967. X, 2 ♀♀ (investigating the ground) 17 July 1968. XIV, ♀ 26 July 1968.

33. *Ectemnius* species.

*Author's records.* — NORTHWEST TERRITORIES. — X, ♀ 31 July 1967. XIII, ♀ 7 August 1967.

Genus *Lestica* Billberg

34. *Lestica producticollis* (Packard).

*Known biology.* — One ♀ found in woods (Krombein, 1952b: 338).

*Known distribution.* — Transcontinental; in Canada and United States in Transition and Upper Austral zones (Muesebeck et al., 1951: 1028; under the name *Solenius producticollis* (Packard)). Alberta (Strickland, 1947: 127).

*Author's records.* — NORTHWEST TERRITORIES. — X, ♂ 9 August 1967.

Tribe Oxybelini

Genus *Oxybelus* Latreille

35. *Oxybelus uniglumis quadrinotatus* Say.

*Known biology.* — Females dig nests in light, friable sand (Evans, 1970: 493). Prey consists of flies of the following taxa: *Symphoromyia* sp.; *Musca domestica* Linnaeus; *Ophyra leucostoma* Wiedemann; *Sarcophaga rapax* Walker; *Hylemya cilicrura* (Ron-dani), and other muscids, and anthomyiids (Evans, 1970: 493; Muesebeck et al., 1951: 1033, under the name *Oxybelus quadrinotatus*). Evans (1962: 477) presents a detailed study of prey-carrying behavior.

*Known distribution.* — Generally distributed throughout the United States and southern Canada (Muesebeck et al., 1951: 1033; under the name *Oxybelus quadrinotatus*).

*Author's records.* — NORTHWEST TERRITORIES. — V, ♀ 14 August 1967. X, ♀ 11 July 1968 (digging in sand); ♀ 25 July 1967 (digging in sand); ♂, ♀ 26 July 1967; 2 ♀♀ 31 July 1967. XI, ♀ 2 August 1967. XIV, ♂ 26 July 1968.

DISTRIBUTION PATTERNS OF THE SUBARCTIC SPHECID  
FAUNA AND FACTORS AFFECTING ITS DIVERSITY

The samples of sphecid wasps from the Yukon and Northwest Territories here discussed indicate that the fauna is impoverished in terms of number of taxa compared with that of more southern climates. These subarctic samples comprise 35 species in 21 genera or subgenera. In contrast, at Jackson Hole, Wyoming (44°N., 5750 feet above sea level at Moran) there are 94 species in 42 genera or subgenera (Evans, 1970), and in Alberta 160 species in 53 genera or subgenera (Strickland, 1947). The latter area is much more extensive and was sampled over a longer period of time than were the subarctic areas described here, so part of the difference in diversity between the two must be the result of these factors.

That the number of species included in most genera is higher farther south than in subarctic areas is illustrated by the following examples. Following each generic name is, first, the number of species from Jackson Hole, Wyoming, and second, the number of species in the subarctic samples: *Podalonia*, 6 vs. 2; *Ammophila*, 9 vs. 3; *Tachysphex*, 5 vs. 3; *Crabro*,

4 vs. 2; *Ectemnius*, 9 vs. 6.

Although these comparisons demonstrate faunal impoverishment over a wide range of latitudes, this phenomenon is not so well marked within the limits of the study area, except perhaps in the Yukon, where the study area extended almost 2° of latitude farther north than in the Northwest Territories study area (see Table 1; localities are listed from left to right, in order of increasing latitude for each study area). A more conclusive comparison should, however, involve both standardization of the conditions of sampling in time, space, and season; and rating of the localities in terms of vegetation, local climate, and soil conditions.

Comparison between rows rather than columns is probably more reliable: it gives an indication of how common and/or widespread each species is, assuming that sampling biases are equally distributed over species or nearly so.

Some groups of sphecids, represented by an abundance of species southward have few species in subarctic regions. For example, there are few Sphecinae in the sample. Of four tribes in this subfamily, only one, the Ammophilini, is represented in the study area. One ammophiline, *Ammophila azteca*, was one of the commonest and most widespread sphecids encountered. Wasps of this genus are also at high latitudes and altitudes in Europe. Another subfamily with many taxa farther south is the Nyssoninae. Of six tribes, only three are represented in the subarctic study areas.

In contrast, the subfamily Crabroninae is well represented, both in numbers of species and in numbers of individuals in these samples (10 species from a total of 35 sphecid wasps, or almost a third; and 39 species from a total of 160 Albertan species, or a quarter). Some subarctic crabronines are Holarctic.

Other wasp groups from the study areas with northern affinities are *Dryudella* (subfamily Astatinae), some Gorytini (species 22 and 23), and some Pemphredoninae (species 10 and 13). The last-named subfamily is represented by six species in my samples. Like crabronines, pemphredonines are very abundant and widely distributed over the study areas.

Some of the species represented in the samples are widely distributed on the North American continent, particularly latitudinally. Some are transcontinental such as *Astata nubecula*, (ranging southward to New Mexico and California) and *Miscophus americanus* (ranging southward to Florida and Texas). Wasps of the tribe Tachytini are well represented in temperate as well as tropical areas of the world. Many are wide-ranging on this continent, for example, *Tachysphex quebecensis* and *T. terminatus* (species 6 and 7). Another species of the genus, *T. aethiops*, is, however, restricted to relatively high latitudes or altitudes. *Cerceris nigrescens* and *Oxybelus uniglumis* also range widely. Among pemphredonines, *Mimesa clypeata* (species 10) and *Pemphredon bipartior* (species 12) are wide-ranging, as are a number of crabronines (species 25, 28, 30, 31, 32 and 34).

Routes of dispersal are probably river valleys for southern-based species, and the north-south trending mountain systems for northern-based species.

In conclusion, the subarctic sphecid fauna comprises elements derived from cold-adapted groups as well as wide-ranging species probably derived from warm-adapted groups. Although diversity is limited, the fauna is nonetheless quite varied for high latitudes. What makes it possible for these insects to live so far north? We do not know, but factors can be suggested, in general terms. Local conditions of climate, soil, vegetation and microclimates are likely important (Corbet, 1969; Geiger, 1965; Uvarov, 1931). An important behavioral adaptation is probably that of basking, which enables a flying insect to accumulate sufficient solar energy even when the air temperature is quite low (Baker and Hurd, 1968; Clench, 1966; Digby, 1965; Downes, 1964; Hocking and Sharplin, 1965; Kevan, 1970; Kevan and Shorthouse, 1970; Monroe, 1956; Parry, 1951; Richards, 1970). Physiological

adaptations to the cold which make possible survival through the winter are also probably important (Aoki, 1956; Asahina, 1959, 1966, 1969; Dubach et al., 1959; Losina-Losinsky, 1962; Salt, 1961; Scholander et al., 1953; Smith, 1961; Sømme, 1964; Tanno, 1964; Ushatinskaya, 1957).

The next phase of study of the subarctic sphecids fauna should aim at elucidating these factors.

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A TAXONOMIC REVIEW OF THE EASTERN NEARCTIC  
SPECIES COMPLEX *PTEROSTICHUS (HAPLOCOELUS) ADOXUS*  
(COLEOPTERA: CARABIDAE)

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9 : 35-40 1973

*Study of selected material of Pterostichus (Haplocoelus) adoxus auctorum shows that two species are included under this name: Pterostichus adoxus (Say), 1823 and Pterostichus tristis (Dejean), 1828. Abbreviated synonymy is presented for each species and lectotypes are selected.*

*L'étude des spécimens de Pterostichus (Haplocoelus) adoxus auctorum montre que deux espèces sont confondues sous ce nom: Pterostichus adoxus (Say), 1823 et Pterostichus tristis (Dejean), 1828. La synonymie est établie pour chaque espèce et des lectotypes choisis.*

When studying the Pterostichini I collected in northeastern United States in 1967-68, I had difficulty identifying two forms of *Pterostichus* subgenus *Haplocoelus*. Specimens of both forms keyed to *P. adoxus* Say (Lindroth, 1966:449). The data presented in this paper show that included in the current concept of *P. adoxus* are two species, named *P. adoxus* (Say) and *P. tristis* (Dejean).

## MATERIAL

I studied a total of about 200 specimens which includes types and other material from the collections listed below and material collected by me. Types for the following nominal species are in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ): *Feronia adoxa* Say, *Pterostichus rejectus* LeConte, *P. subarcuatus* LeConte, and *P. sustentus* LeConte. Type material for the following nominal species described by Casey is in the National Museum of Natural History, Washington, D. C. (USNM): *P. zephyrus*, *P. tetricula* and *P. sufflatus*. Type material of *Feronia tristis* Dejean is in the Oberthür Collection, Museum National d'Histoire Naturelle, Paris (MHNP). I also studied specimens from the collection of J. Nègre, Versailles, France.

## METHODS

Specimens were compared with one another by examination of external characteristics, by measurements and by examination of the male genitalia.

The following measurements were made: (1) overall length; specimen extended from apex of elytra to apex of mandibles. Few female specimens were available and no differences were discovered between sexes. Thus, all specimens studied, male and female, are considered together. (2) distance of posterior lateral seta from adjacent hind angle: h; measured parallel to longitudinal axis of pronotum.

Mensural data are presented in the form of a histogram (Fig. 1) and a scatter diagram (Fig. 2). Form of pronotum and median lobe are illustrated by line drawings made with a stereobinocular microscope and camera lucida.

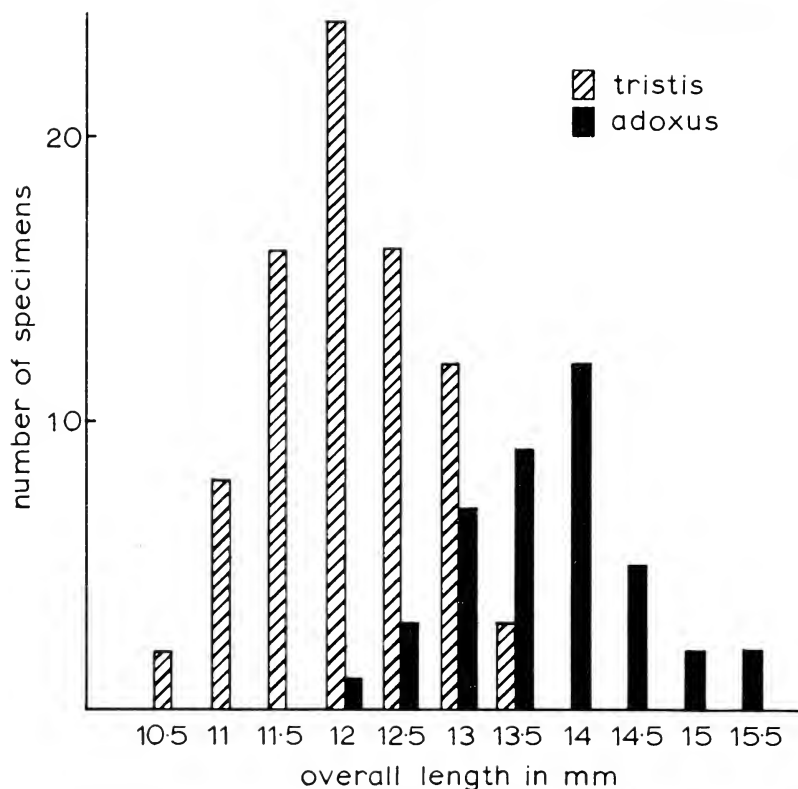


Fig. 1. Histogram illustrating variation in overall length (mm) for selected material of *P. adoxus* and *P. tristis*.

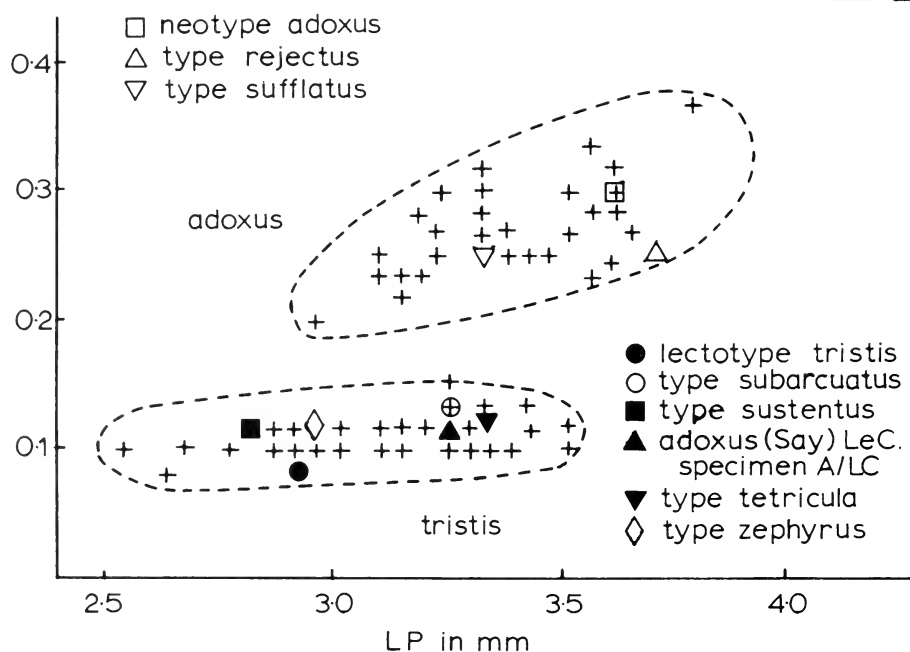


Fig. 2. Scatter diagram illustrating differences in the relationship between length of pronotum (LP) and distance of posterior lateral seta from the hind angle of the pronotum (h) for selected material of *P. adoxus* and *P. tristis*.



## RESULTS AND DISCUSSION

The specimens available for study are arrayed in two groups, as indicated by differences in measurements and ratios (Fig. 1 and 2), in pronotal form (Fig. 3 and 4) and in the form and proportion of the median lobe (Fig. 5-8). Table 1 includes a summary of these data plus additional, less definitive diagnostic characteristics, the most distinctive being No. 4, 5, and 9. The names used are the oldest available for each of these groups.

Table 1. Characteristics and character states for distinguishing between *P. adoxus* and *P. tristis*.

Characteristic	Character state	
	<i>P. adoxus</i>	<i>P. tristis</i>
1. Overall length	12.0-15.5 mm (mean 14.0 mm)	10.5-13.5 mm (mean 12.0 mm)
2. Color of integument	black	brown
3. Head: fronto-clypeal suture	absent or, if visible, not impressed	impressed, at least laterally
4. Pronotum: posterior-lateral seta	remote from hind angle (Fig. 2)	close to hind angle (Fig. 2)
5. Pronotum: base between posterior-lateral impressions	longitudinally wrinkled	smooth
6. Pronotum: hind angle	obtuse	right, slightly protruding laterally
7. Pronotum: lateral grooves	widened anteriorly, absent near hind wings	narrower anteriorly
8. Elytra: basal margin	straight laterally	bent forward laterally
9. Male genitalia: median lobe	straight ventrally (Fig. 6a, 7a); apex shorter and more rounded at tip (Fig. 6b, 7b)	ventrally swollen at middle (Fig. 5a, 8a); apex longer, narrowly rounded (Fig. 5b, 8b)

Evidence that these groups are probably specifically distinct is provided by the geographical distribution of each. Specimens of the *adoxus* type occur in an area from south Quebec and Maine to Pennsylvania, along the Appalachian Mountains. From the few available data, no altitudinal limits can be set. However, all the specimens I have seen were collected below 800 m. Specimens of the *tristis* type are found in an area extending from southern Canada to Georgia and from the east coast to Wisconsin, both in the mountains and in the lowlands. The specimens I have seen were collected from sea level (Eatontown, Monmouth County,

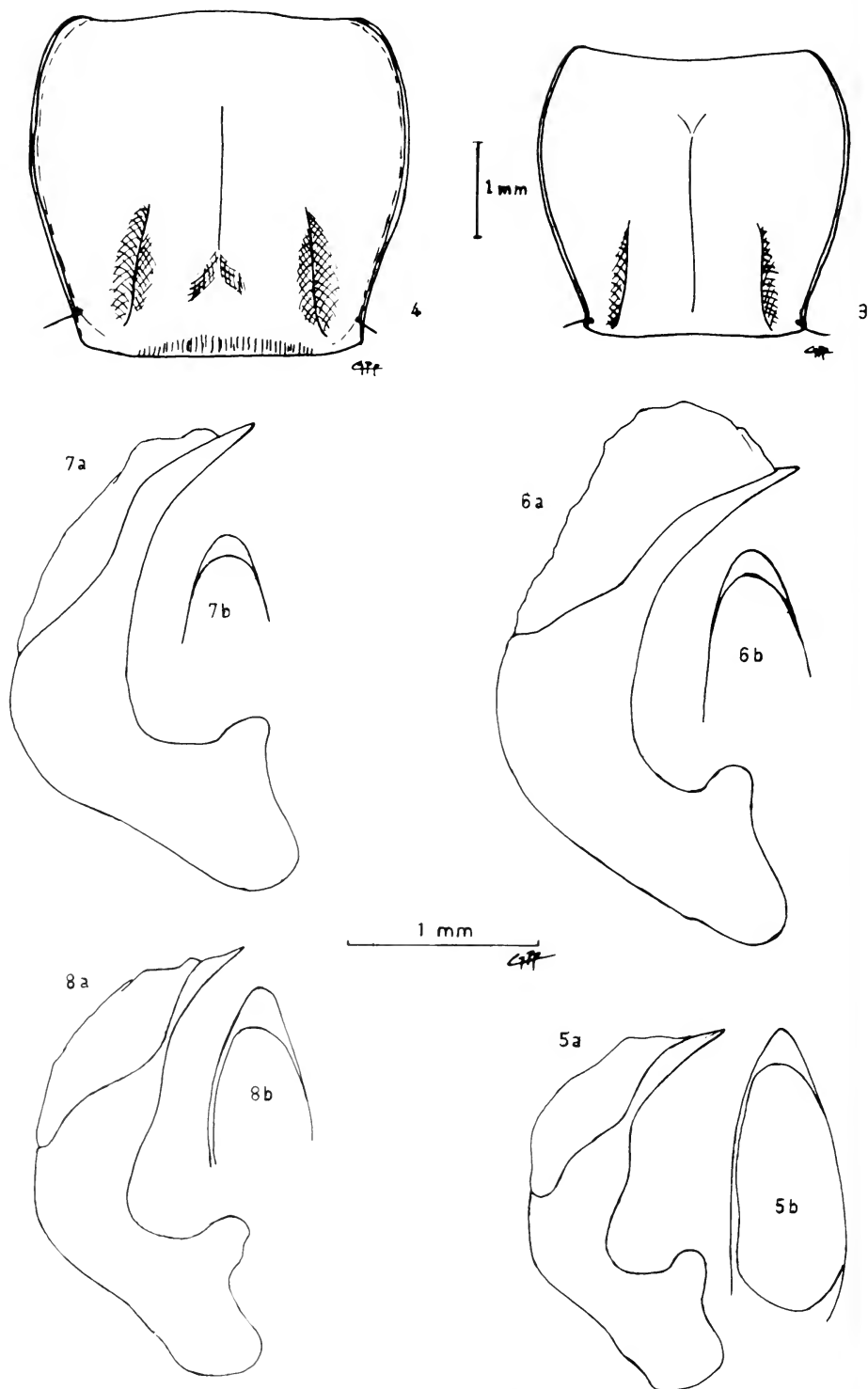


Fig. 3-4. Pronotum, dorsal aspect. 3, *P. tristis*; 4, *P. adoxus*. Fig. 5-8. Median lobe; a — left lateral aspect; b — apex, dorsal aspect. 5, *P. tristis*, Lectotype; 6, *P. adoxus*, Neotype; 7, *P. rejectus*, Lectotype; 8, *P. tristis*, specimen A/LC in LeConte collection.

New Jersey) to 2000 m (Mt. Mitchell, Yancey County, North Carolina). A specimen labelled "Texas", *ex* Collection Sicard in MHNP, is probably mislabelled. The two groups are sympatric over a wide area and I have collected both in the same habitat at the following localities in the United States: NEW YORK: Ulster Co., Claryville, Catskill Mountains (800 m). NEW HAMPSHIRE: Carrol Co., Jackson, White Mountains (300 m). MAINE: Piscataquis Co., between Millinocket and Mount Kathadin (500 m).

H. Goulet (*personal communication*) found the two species together at Lac des Isles, about 60 miles north of Montreal, Quebec, about 200 m elevation and noticed that in that locality *P. tristis* was found only under the bark of fallen deciduous trees and *P. adoxus* on soil under stones. Specimens with intermediate combinations of characteristics are not known. Thus, although populations of these two groups live in close proximity they probably do not interbreed, and therefore they are probably specifically distinct.

#### SYNONYMY AND TYPE SELECTION

##### *Pterostichus adoxus* (Say)

*Feronia adoxa* Say, 1823:46. Neotype in MCZ. (For details see Lindroth and Freitag, 1969: 340).

*Pterostichus rejectus* LeConte, 1852:236. Lectotype, here selected, male, labelled "type; 5612". No locality data. Two paralectotype females (MCZ).

*Pterostichus sufflatus* Casey, 1920:187. Lectotype, here selected, female, labelled "TYPE NO. 47040". No locality data. (USNM)

##### *Pterostichus tristis* (Dejean)

*Feronia tristis* Dejean, 1828:324. Lectotype, here selected, first specimen in front of *adoxus* box label in the Oberthür Collection, labelled as follows: "♂, LeConte; *adoxus* Say *tristis* mihi exarata mihi alim, in Amer. Bor., D. LeConte" (labels on green-colored paper, handwritten by Dejean). (MNHP)

*Feronia interfactor* Newman, 1838:387. NEW SYNONYMY. Type material should be in the British Museum (Natural History), but R. B. Madge (*in litt.*) could not find it there, and Lindroth (1966:467) believed it to be lost. The evidence for this proposed synonymy is, therefore, indirect. It is derived from label data associated with a male *P. tristis* (here designated specimen A/LC; Fig. 2 and 8), in the LeConte collection. This label reads "*adoxus* (Say) LeC, *tristis* (Dej.), *interfactor* (Nw)". It indicates to me that LeConte was familiar with the Newman material and that he regarded it as conspecific with *P. tristis*. It also suggests that at the time this specimen was labelled, LeConte did not regard the three species described by him (*P. rejectus*, *P. sustentus* and *P. subarcuatus*) as conspecific with *P. adoxus*, although he did synonymize all of these names in 1873 (p. 304).

*Pterostichus sustentus* LeConte, 1852:236. Lectotype, here selected, female, labelled "type; orange disc [southern states]; 5611". One paralectotype female, same data (MCZ). NEW SYNONYMY.

*Pterostichus subarcuatus* LeConte, 1852:238. Lectotype, here selected, female, labelled "type; pink disc [middle states]; 5618". (MCZ). NEW SYNONYMY.

*Pterostichus zephyrus* Casey, 1884:2. Lectotype, here selected, male, labelled "TYPE NO. 47041". No locality data. (USNM). NEW SYNONYMY.

*Pterostichus tetricula* Casey, 1913:130. Lectotype, here selected, female, labelled "Bayfield, Wisc.; TYPE NO. 47039". (USNM). One paralectotype, female, same locality. NEW SYNONYMY.

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## Book Review

SWAN, L. A. and C. S. PAPP. 1972. The common insects of North America. Harper and Row, Publishers, New York, Evanston, San Francisco, London. xiii + 750 pages, text-fig. 1-1422, 8 color plates, 2 appendices, glossary, bibliography, indices of subject and common names and of scientific names. Price \$15.00 U. S. A.

According to the authors, the purpose of this volume is to provide an easy way to identify the more common insects of North America north of Mexico, emphasis being placed on comparison of specimens with illustrations. According to a statement by the publishers on the dust jacket, the volume is of "special interest because of its thorough coverage of Canada."

The text consists of an introduction of 32 pages, a "pictured key" to the insect orders and chapters 1 to 23, each dealing with the taxa of a single order.

The introduction, designed to enlighten those potential users of the book who have not had the benefit of formal training in systematic biology or in entomology, explains classification of the animal kingdom and locates the insects and other arthropod classes in the general system. Binomial nomenclature is touched on, and the usual erroneous statement is made that Linnaeus devised this system. Insect structure, function, and development are discussed briefly but reasonably well. Many structural features are illustrated with fully labelled line drawings. The introduction concludes with an excellent, 1.5 page discussion of the value of insects to ecosystems in general, and to man: as pollinators, as agents of biological control of plants and of other insects, and as items of diet.

On page 3, the authors chide "people" who err in that they "do not think of insects as animals . . .". On page 10, the authors make a similar error when they refer (line 5) to "man and animals." The statement should be "man and other animals."

The authors neglect to inform their readers that because of the small size of most insects, optical equipment might be required to examine a specimen in sufficient detail to make a meaningful comparison with the illustrations and data provided in the text.

In discussing classification, the authors use the terms "broken down" and "divided" to refer to the process of classifying. In reality, classification consists of organizing discrete entities into collective groups, and further grouping of the initial groups. The terms in quotation marks are without meaning in classification.

The "pictured key" consists of 15 pages of illustrations and brief descriptive statements numbered sequentially, about the characteristics of each order. There are no directions for proceeding from one step to the next. A key, on the other hand, is a flow sheet, with specific directions at each point. In this section, pictures there are; key there is not.

Twenty-three orders are treated in the text. It appears that the authors used as a model for the sequence of orders some publication produced prior to 1950. To many it might seem immaterial that an antiquated system is used, but to me it seems unreasonable to return to an arrangement clearly discordant with those proposed in the more recent literature.

The book treats superficially and illustrates specimens of about 1,500 species, about 1.5 percent of the North American insect fauna. The species represent 276 families.

Each family is characterized structurally and biologically in about one half page of text. Within each order, most species represented by figures are numbered. For each numbered species, data given are common name (in boldface), scientific name, geographical range, a brief description of adults (including size in inches to one or two decimal places) and larvae, and some information on biology. Economically important species are noted. For some groups, keys are given (for example, worker termites of eight genera).

The number of species treated per supraspecific taxon depends in part upon conspicuousness of individuals and popularity of the group with collectors. For example, specimens of

296 species of Lepidoptera are figured, included in 44 families. On the other hand, only 111 species of Hymenoptera are figured, included in 35 families. Three of four genera of North American tiger beetles are treated, including 12 species of *Cicindela*. In eight pages, 26 species of coccinellid beetles are treated, and figures are provided of an additional 36 *Hyperaspis*, 11 *Scymnus* and six *Hippodamia* species. Butterflies fare well, also: 153 species, in 51 pages.

In general, the illustrations adequately represent the aspect of the specimen figured. Each figure is numbered, and associated with each is a vernacular name in capital letters, the scientific name in italics and an indication of the size of the specimen. The color plates are technically satisfactory, but they add little of value. Many of the insects illustrated in color have been so illustrated previously.

Appendix I is a four page synopsis of a portion of the geologic time table, beginning with the Devonian Period and ending with the Quaternary, summarizing major geomorphic events (excluding continental drift), and major biological ones, including appearance of the insect orders.

Appendix II is a list of names of orders and families represented in the book. Both this and the glossary are useful.

A volume of this sort might be expected to serve as an entry to point to the entomological literature on identification. Normally, this is accomplished by references in the text keyed to a bibliography. Although the latter is provided, there are no text-references. Thus, a person wanting to know more about, say dragonflies, has to fumble through 17 pages of references to discover the publications by Needham and Westfall, and Walker.

The bibliography comprises two portions: one, labelled "General," the other, "Technical." This distinction eludes me because the categories must overlap by definition (many "general" works must also be "technical") and because I was unable to discern criteria used by the authors in assigning publications to one of the two groups. But this is a minor objection. More important, the basis for inclusion or exclusion of references is not apparent. It seems that no systematic effort was made by the authors to list the recent taxonomic literature of major consequence to their work, or to be consistent about what was included. For example, Swain's "Insect Guide" was included, but the more recent "Field Guide to the Insects" by Borror and White was excluded. "A Key to the Wyoming Grasshoppers" was included, but the "Acridoidea of southern Alberta, Saskatchewan and Manitoba" was excluded. The revision of *Meloe* by Pinto and Selander was included, but the revision of the meloid genus *Epicauta* by Werner was excluded. A list of this type could be extended. Another criticism is that no consistent sequence is used for listing several publications by the same author: for some, the earliest publication is listed first; for others, the latest; for still others, no arrangement is perceivable.

The planning denied to preparation of the bibliography is further illustrated by the body of information associated with the periodical cicadas. The authors devote a bit more than two pages of text to these species (pages 133-135), including a map and a table, based on a USDA Economic Insect Report (cited in the text, but not in the bibliography). In spite of the importance accorded by the authors to this species complex, they do not cite the important taxonomic paper by Alexander and Walker entitled "Evolutionary relationships of 17-year and 13-year cicadas . . .", in the Miscellaneous Publications, Museum of Zoology, University of Michigan, No. 121, 1962.

The bibliography would be of greatest value if the publications were arranged by taxonomic groups because the purpose of this book is to enable a person to identify insects; part of this task is to locate relevant references. In spite of these shortcomings, I found this section interesting because it contains references to many papers that had previously escaped

my notice.

How does one distinguish a "common insect" from an uncommon one? The authors neglect to provide this information, and thus do not inform the readers of the basis for inclusion or exclusion of taxa. For the beetles, I think I was able to deduce one of the criteria, by comparison of illustrations with those in Jaques' book, "How to know the beetles." There was a remarkable degree of overlap among the species illustrated (and remarkable similarity of illustrations of the same species between the two books). Also, illustrations of ichneumonids are strikingly similar to those in "Ichneumon flies of America north of Mexico" by Townes and Townes. I suggest that one of the criteria for inclusion of a species was that it had been illustrated in a previous publication. The illustrations were no doubt drafted by the authors, but I believe that many were based on previously published illustrations rather than on insect specimens.

Comparison with illustrations in a book is a successful technique of identification only when the taxa of most specimens that might be referred to it are represented therein by figures. If a person who uses the book cannot know what a "common insect" is he cannot know that a specimen in hand represents a species described in that book. Because criteria for commonness are not established, specimens of any of the 90,000 or so species of North American insects might be referred to this volume which deals with only about 1,500 species. Because of the resulting low degree of probability of actually being able to identify insects to species with this book, and because the authors place emphasis on species identification, the volume seems of limited value for its announced purpose — and so I believe it is. It could play a useful role in identification of higher taxa, but for this purpose its coverage is limited.

A book of moderate size intended to guide one in identifying material drawn from a large fauna should not pretend that its operational level is the species. The family level is realistic. Borror and White's "A Field Guide to the Insects of America north of Mexico" (Houghton Mifflin Company, Boston) is a guide to the families. It is concisely written, superbly illustrated by drawings based on specimens, has a list of references arranged by taxa, and costs only \$5.95. This is the volume for anyone needing to make identifications, who does not recognize the families at sight.

What is the value of "The Common Insects of North America" for Canada? I bring up this point only because of the publishers' statement about "thorough coverage" of this fauna. The coverage is in no sense thorough. Some important forest and crop pests in Canada are not mentioned, and for those that are, brief notice is given and little of it is specifically relevant to Canada. For many species, there is no indication as to their Canadian distribution. I do not blame the authors for this misstatement. It is just one more example of "truth in advertising" as this concept is currently understood by North American business interests. It is a pity that authors need risk their reputations by association with firms whose advertising personnel are unable or unwilling to distinguish between truth and falsehood.

Who needs this book? Entomological bibliophiles and libraries intent upon acquiring complete holdings of entomological literature need it. The experienced entomologist, amateur or professional, who understands its severe limitations, might like to have a copy because the many illustrations facilitate identification, or one might find an interesting reference by browsing through its bibliography. The book, I think, creates its own niche, rather than filling one based on need of those interested in entomology.

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URSPRUNG, H. and R. NÖTHIGER (Editors). 1972. The Biology of Imaginal Disks. Volume 5 in: Results and Problems in Cell Differentiation. A series of Topical Volumes in Developmental Biology. Springer-Verlag, New York, Heidelberg, Berlin. xvii + 172 pp., 56 figures, 12 tables. Cloth 8vo \$14.60 (U. S.).

This monograph reviews recent research on insect imaginal discs — chiefly those of Diptera-Cyclorrhapha and principally those of *Drosophila* species. The book contains six review articles, each with its own bibliography: (1) R. Nöthiger: The larval development of imaginal discs, (2) W. Gehring: The stability of the determined state in cultures of imaginal discs in *Drosophila*, (3) A. García-Bellido: Pattern formation in imaginal discs, (4) H. Ursprung: The fine structure of imaginal discs, (5) J. W. Fristrom: The biochemistry of imaginal disc development and (6) H. Oberlander: The hormonal control of development of imaginal discs. Although each article stands alone, there is considerable overlap, particularly in the first three contributions. All of the authors are productive contributors to the subject reviewed and are former students or associates of Ernst Hadorn, the Swiss embryologist who first realized the heuristic value of imaginal discs and to whom the book is dedicated. D. Bodenstein, in a eulogy recognizing Hadorn's 70th birthday, summarizes his contributions at the beginning of the book. A fuller account together with lists of his publications and theses done under his direction can be found in Chen, P. S., P. Tardent and H. Burla. 1971. Ernst Hadorn zum siebzigsten Geburtstag. *Revue Suisse de Zoologie* 79: 5-28.

One of the principal lacunae in our understanding of development in insects and other eucaryotes is that of cellular determination. How are different cells, all containing the same genetic information in their chromosomes, programmed for a specific fate during development? An answer to this question has awaited a fuller understanding of how genes work at the molecular level and the discovery of appropriate, eucaryote, experimental systems. Practitioners of the science of biochemical genetics have come a long way towards providing the first, while the imaginal discs of holometabolous insects seem to constitute the second.

Experimental imaginal disc research began when Ephrussi and Beadle developed a technique for transplanting discs dissected from donor larvae of *Drosophila* into larval or adult hosts by means of a micropipette. When a disc is transplanted into a larva of the same age as the donor, it develops synchronously with the host and undergoes metamorphosis within it. On emergence of the adult the implant can be removed and examined. In all experiments, the discs were found to differentiate *autotypically*, i.e. into the structure for which the disc was originally determined. Similar results were obtained with fragments of discs, indicating that each disc of the third (last) larval instar contains a mosaic of different cell groups, each determined to form a specific part of the adult structure.

One of the principal advantages of using *Drosophila* species in this work is the availability of a large number of genetic marker mutations. These can be easily recognized by their effect on imaginal surface structures exemplified by coloured, crooked, or multiple hairs, microtrichiae, and bristles.

Discs may be dissociated enzymatically or mechanically into small groups of cells or into single cells. If such cells from identical discs of different mutant donors are mixed together and injected into a wild-type host larva it is found, after metamorphosis, that the cells from different donors collaborate to form normal but mosaic adult structures. The contributions of individual cells to the development of the whole structure can be recognized because they differentiate into bristles and hairs having the colour and shape of the donor phenotype.

Evaluation of other experiments involving the mixture of mutant cells from dissociated discs of different kinds (e.g. wing and leg; haltere and eye-antenna) showed that a cell from



a given disc will only associate with other (*isotypic*) cells from the same kind of disc and not with those (*heterotypic* cells) from other kinds of discs. The association of isotypic cells and separation of heterotypic cells is considered by Gehring to be achieved by cell migration and selective adhesion of cells.

If imaginal discs are transplanted into the abdomens of adult flies rather than into larval hosts, they proliferate into blastemas. The host's haemolymph serves as a culture medium which allows proliferation but does not induce differentiation, probably because of the absence of ecdysone. Such blastemas can be cultured indefinitely by dissecting them from the host fly every two to four weeks, cutting them into fragments and injecting the fragments into fresh host flies. Other fragments are injected into host larvae where they undergo differentiation on metamorphosis of the host. These larval "test implants" provide information about the capacities of the cultured cells for differentiation. Using this technique, Hadorn and his students have shown that the cultured cells maintain their capacity for normal (auto-typic) differentiation even after several years of culturing, i.e. they maintain their state of determination.

However, in cultured blastemas, occasional changes in cell heredity affecting determination occur. Some of the cells, when tested in larvae, at metamorphosis differentiate *allotypically* into organs *other* than those for which the cells were originally determined. For example, a fragment of genital disc blastema might differentiate into antennal or leg structures. This change in cell heredity is called *transdetermination*.

Using these culturing techniques Hadorn's group showed that for each state of determination in a particular disc, there exists a probability of transdetermination in a specific direction. Sometimes these changes in prospective fate are reversible, sometimes not. The only factor so far detected which influences the frequency of transdetermination is proliferation. This suggests that cell divisions are a necessary prerequisite for it.

Naturally-occurring developmental abnormalities leading to the same effect as transdetermination can be induced by homoeotic mutations. A common example is *aristapedia* in which the arista of the antenna is replaced by a tarsus. Gehring suggests that a single mutant "switch" gene could bring into action all the genes necessary for the differentiation of a leg disc in a blastema previously determined to form head structures. Some homoeotic mutations are temperature-sensitive. Temperature-sensitive alleles of the mutation *ss<sup>a</sup>*, for example, cause parts of the antennal disc to develop into leg structures at 16°C and into antennal structures at 25°C with the temperature-sensitive period lying in the third-instar. Gehring suggests that the main problem for future research is the identification of the carrier of determination.

In cyclorrhaphous Diptera, the somatic cells exhibit pairing of homologous chromosomes similar to that occurring at synapsis during prophase I of meiotic cells. By treating prophase cells with X-rays it is possible to induce mitotic recombination in them. Strains of *Drosophila* are used which are heterozygous for a recessive marker gene. If a cell is irradiated just before it divides, crossing-over may be induced such that one or both of the daughter cells become homozygous with respect to the mutant gene. The clone of cells arising from this initial daughter cell will, with subsequent development, appear in the adult as a patch of mutant tissue surrounded by wild-type tissue.

Using this technique Schneiderman and García-Bellido and their students have shown that oriented cell divisions, differential mitotic rates, and local differences in cell size are all involved in producing changes in form in the discs during their development. They have also shown that determination is a gradual, progressively-narrowing phenomenon. By irradiating individual cells at different stages of development and then following what happens in the irradiated area, these workers have been able to determine the number of blastoderm cells

in the embryo that give rise to each imaginal disc and to prove that determination of adult structures begins during blastoderm formation.

Experiments using gynandromorph tissue can yield the same kind of information. Gynandromorph tissues are mosaic and contain both male and female cells. In *Drosophila* they arise when one of the two X-chromosomes is lost during development of a female embryo, resulting in female (xx) and male (xo) tissue patches. If the insect was originally heterozygous for x-linked cell marker mutations affecting bristle colour or shape, for example, the mosaic is recognizable on the body surface of the adult fly because the recessive mutations are uncovered through the loss of wild-type alleles. Though gynandromorphs are rare in nature, they can be induced artificially in various ways.

Studies of the ultrastructure of imaginal discs, as reviewed by Ursprung, have revealed no differences between cells of different discs. They have yielded evidence suggesting that the surface increase accompanying disc eversion in the pupal stage results largely from a change in shape of the epithelial cells comprising the disc; in larvae they are columnar; in pupae cuboidal. Some mutants of *Drosophila* lacking portions of or complete appendages in the adult have imaginal discs in which many cells die during development. Others have smaller than normal discs.

As emphasized by Fristrom and Oberlander, *Drosophila* imaginal discs are almost ideal material for studying the biochemical effects of hormones on differentiating tissues. They are easy to culture *in vitro* and their only disadvantage, their small size, has been overcome by the perfection of mass isolation techniques (up to 220,000 discs per day). Since synthetic juvenile hormone and ecdysones are commercially available, many breakthroughs in our understanding of the biochemistry of development are in the offing. Fristrom and his colleagues have found that  $\beta$ -ecdysone is much more active than  $\alpha$ -ecdysone in inducing the synthesis of RNA, principally ribosomal, in cultured discs. Ecdysone apparently enters the disc cells where it directly affects transcription. No "second messenger" such as cyclic AMP which mediates the action of several different hormones in vertebrate systems has been found. Increased protein synthesis results from increased RNA synthesis and these proteins probably participate in the orientation, assembly, or function of microfibers evoking the change in cell shape causing appendage eversion during pupation. It was formerly thought that blood pressure was responsible for eversion *in vivo*, but discs evert just as successfully when removed and cultured *in vitro* with  $\beta$ -ecdysone. Juvenile hormone acts directly and antagonistically with ecdysone on both synthesis and eversion. Younger discs are less sensitive to both juvenile hormone and ecdysone than mature discs. If discs are cultured with fat body or in media conditioned with fat body, the effects of both juvenile hormone and moulting hormone are more rapid, suggesting that the fat body may influence the acquisition of competence by the disc.

Disc research has become a meeting ground for geneticists, developmental biologists, entomologists, biochemists and endocrinologists. Thus, this book deserves and will probably have a wide circulation. Although it is well produced, the book has several errors in typography and style ("prepupal" is usually spelled "prepupal" and "for example" is always abbreviated whatever the context). Some contributors to the book (e.g. García-Bellido) presuppose more background on the part of their readers than do others (Gehring, Fristrom) and some (Fristrom) write more clearly. A detailed table of contents compensates in some measure for the lack of both author and subject indices.

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## Book Review

D'ABRERA, B. 1971. Butterflies of the Australian Region. Lansdowne Press Pty Ltd., Melbourne. 416 pp., 2362 color photographs, two pages of maps, three groups of line drawings in the text, glossary, 160 references, index, one page corrigenda, one loose insert errata. Size 13¾" x 10¼", hard covers. Printed in Hong Kong. Price: \$39.95 in the U. S.

Since Fabricius (1775) first described species of Lepidoptera from Australia, several accounts have appeared summarizing knowledge of this fauna. The most extensive of these is volume IX of Seitz's (1927) "The macrolepidoptera of the World, The Indoaustralian Rhopalocera". D'Abnera's "Butterflies of the Australian Region" is the first work to figure all known species of butterflies inhabiting Australia, New Guinea, the Moluccas, New Zealand, and the South Pacific islands. Included are Lepidoptera of the following families: Papilionidae, Pieridae, Danaidae, Nymphalidae, Libytheidae, Satyridae, Amathusiidae, Lycaenidae, and Riodinidae. The family Hesperidae is excluded.

The book is organized into two parts, introductory and systematic. The first part includes short notes on how the text is organized, butterfly life history, mimicry and protective coloration, variation, nomenclature and classification. The history of lepidopteran collecting and study in the Australian Region is briefly summarized. This section including glossary is 39 pages long with 3½" wide margins on most pages. These margins are partly occupied by 13 groups of photographs and diagrams.

The second part, entitled "A guide to the identification of the butterflies of the Australian Region", provides data about and photographs of adults of more than 900 species. The figures are color photographs of specimens deposited in various museums. Most figures are of dorsal aspects. In addition, illustrated are the ventral sides, morphs of polymorphic species, and some immatures. Keys are not included and identifications must be made by comparing specimens with figures. Ninety-one specimens represent "types" (indicated by a red dot opposite the specimen), and six represent paratypes (indicated by a yellow dot). Fourteen taxa are described as new: three species and 11 subspecies.

The following data are given for each species: binomen and author, reference to original description, abbreviated synonymy, geographic range, status, races, depository for figured specimens, life history stages, and short description of known ones, and food plant, if known. On each page, the text is marginal. Each illustration is beside the text relevant to it.

This volume is little more than an updated illustrative companion to Seitz's "Indo-australian Rhopalocera". The sequence of arrangement of taxa, in general, is antiquated. The illustrations are of good quality, but the scale at which the individual photographs are reproduced is not indicated and the statement on the cover flap, qualifying these as "natural size" is untrue. For example, *P. demoleus sthenelus* figured on page 41, is shown to have a wingspan of 20 inches. Because illustrations are unnumbered and no list of illustrations is provided, figures in the first part can be located only by searching through the text. In the systematic section they can be found by locating the name of the relevant taxon in the index. While many of the photographs portraying immatures or adults in their natural habitats are first rate, some like that on page 48 should not have been included, for they show nothing worth recording.

Poor layout reduces the value of many of the photographs. This is particularly true of figures where the center fold cuts through the right half of the butterflies illustrated. The marginal half of most pages is reserved for the text accompanying the figures in the systematic part. The high price will hamper the sale of this book in a highly competitive market. Three other books were published on the same subject within the last three years, though

each with different emphasis. In spite of its shortcomings, "The butterflies of the Australian Region" is an important reference for lepidopterists.

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Publication of *Quaestiones Entomologicae* was started in 1965 as part of a memorial project for Professor E. H. Strickland, the founder of the Department of Entomology at the University of Alberta in Edmonton in 1922.

It is intended to provide prompt low-cost publication for accounts of entomological research of greater than average length, with priority given to work in Professor Strickland's special fields of interest including entomology in Alberta, systematic work, and other papers based on work done at the University of Alberta.

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# Quaestiones

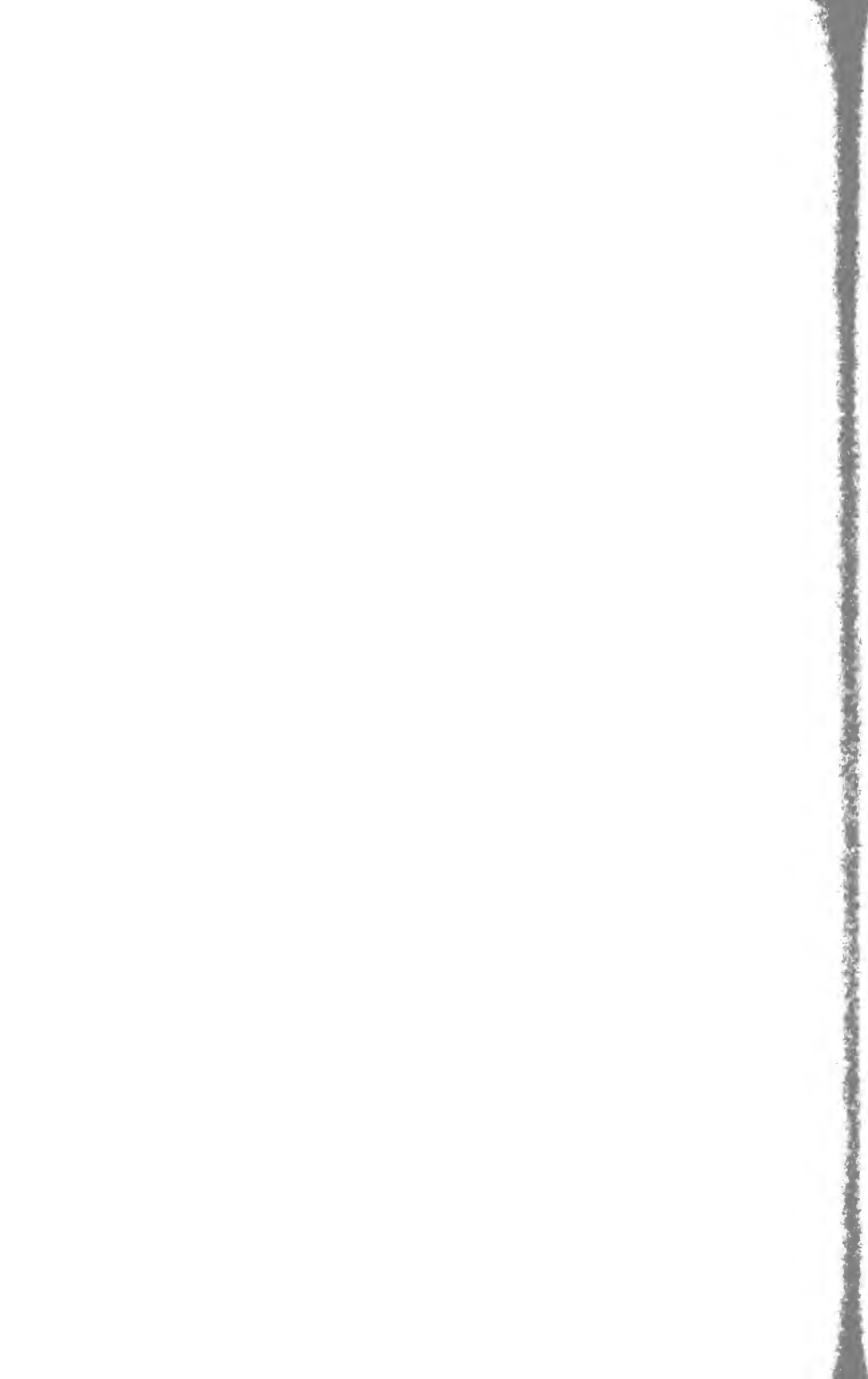
# entomologicae

A periodical record of entomological investigations,  
published at the Department of Entomology,  
University of Alberta, Edmonton, Canada.

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QUAESTIONES ENTOMOLOGICAE

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### Editorial — For Love or Money?

One of the more unfortunate features of our life and times is the increasing difficulty of finding anybody willing to do anything without being paid for it, preferably at the going rate or better. This is perhaps not surprising in respect of daily toil or labour involving the sweat of the brow or the mobilizing of the mind but it becomes somewhat absurd when extended to such supposedly enjoyable activities as the playing of games and even to being entertained. This situation arose as a side effect from the efforts of organized labour to improve the lot of the so-called working classes. They have been laudable efforts, towards an objective with which I have no quarrel; but I have said so-called working classes because I think this term needs re-definition for our present day and age. It was introduced at a time when the population of many countries could be divided into two groups, one much larger and less influential, those who worked for a living; and the idle rich. In our present day populations we have plenty of idle and plenty of rich but these two qualities are less frequently found in the same person than they used to be. The so-called working class of today includes a substantial segment, perhaps best referred to as the idle poor, who no longer work

but who apparently enjoy a modest existence on funds from welfare, unemployment insurance, or some more oblique dispensation of the taxpayer's money. It seems necessary to assume that such people either do not like work of any kind or at least have been unable to secure work of a kind which they might enjoy. We may mention in passing that management involves work.

Another result of the efforts of organized labour to improve the lot of the working classes has been to change the meaning of the terms professional and amateur so that they become essentially antithetic. A person who gets paid for what he does is a professional, a person who does not is an amateur. In their original meanings these words were far from antithetic. Professional meant simply a person, who, by public declaration or otherwise through his training or official qualifications, indicated his intention and presumably ability to fulfil a certain role. An amateur was a person who filled a certain role, although perhaps not one recognized by society, simply because he loved filling it. The assumption that a person who does something without being paid for it loves doing it, may or may not be justified. A third pair of meanings of these two terms, also antithetic and recently acquired, makes the professional a person who does a good job and the amateur a person who does an indifferent one. These last meanings are in direct conflict with the original ones since, in my experience, one is more likely to get good work done by a person who loves doing it than by a person who is merely doing it for the money. It is principally for this reason that it is unfortunate that people willing to do things without being paid for it are becoming increasingly scarce.

While entomology has certainly not been immune to the reduction in its population of amateurs, it is my impression that it has suffered less than most other branches of scientific work. Certainly it appears likely that there will be plenty of opportunity for amateurs, in the two best senses of the word, to work in the field of entomology for many years to come. This has many advantages. In the first place, amateurs in a field help to keep it in touch with the public. Perhaps more important is the increasing proportion of our time available for leisure activities promised us by technological advance for some time now, though many of us see little sign of fulfillment of this promise. One of the dangers of this increased leisure is that it can lead people to accept, by way of regular employment, something which they are not really interested in doing, thus increasing the risk of them becoming members of the idle poor. Since routine, humdrum, repetitive occupations are clearly those most readily taken over by machines and computers, it would seem reasonable to expect technological advance to make it easier for people to find more enjoyable and interesting occupations than in earlier days, but there is no clear evidence that this is so. Perhaps this is because there are too many people and not enough things that need doing. Or could it be that the possibility of survival without work has been selecting for survival those people who can get no enjoyment out of work of any kind, the hard-core of the idle poor? If so, what price a guaranteed minimum income? I would suggest the smaller the price, the better. Amateurs, in the original sense, are enthusiastic people; enthusiasm is infectious and one of the most important qualities to be sought in a teacher.

Dr. Ruby Larson has always been an enthusiastic person. Her first employment was as an impoverished country school teacher in Saskatchewan. From that position, she took a summer school course in biology from Dr. J. G. Rempel, then Professor of Biology at the University of Saskatchewan, now fulfilling a similar role from retirement at the University of Victoria. This convinced her that biological research was the most exciting occupation in the world. While a student at the university, she found summer employment counting wheat chromosomes at the Swift Current Experimental Station of the Canada Department of Agriculture in connection with the cereal breeding work being conducted there by A. W. Platt and Chris Farstad. This eventually led to her appointment as a cytogeneticist and her work

in this field in relation to the resistance of plants to insect and other damage is well known. Nobody however, who has been in contact with Dr. J. G. Rempel could escape some enthusiasm for entomology. These two enthusiasms still constituted only a part of the total enthusiasm which Dr. Larson put into the formation and operation of the Junior Science Club of Lethbridge. Characteristically, she attributes the success of this club to the young people who joined it but, going back to first principles, the young people who joined it did so because of her enthusiasm. This enthusiasm also drew collateral support for the Club from her colleagues at the Canada Department of Agriculture Research Station in Lethbridge and elsewhere.

The authors of all three papers in this issue of *Quaestiones entomologicae* were members of Dr. Ruby Larson's Junior Science Club of Lethbridge. As she puts it, the remarkable thing is not that they became entomologists, that was inevitable, but that all three of them have followed their first main interest; David Larson with his beetles mainly because of their beautiful structure; Ken Richards with his bees partly because of his association with Gordon Hobbs; and Joe Shorthouse with his insect galls. It is of special interest that the Larson paper is doubly amateur, representing as it does, the work of J. B. Wallis, in his day one of Canada's leading amateur entomologists. The breadth of interest of the Club is reflected in the fact that doctors, teachers, architects and engineers, in addition to entomologists, have come from among its members. It is for this and other reasons that we are pleased and proud to dedicate this issue of *Quaestiones entomologicae* to Dr. Ruby Larson, personality, teacher, scientist, biologist, cytogeneticist, and entomologist; professional and amateur, in the best senses of both words, in all of these fields.

The story of Ruby Larson is a story of what the enthusiasm of an amateur, in the original sense of the word, can accomplish. It is also a story of the influences of teachers on students, Rempel, via Larson, on many others. Such influences, as H. T. Pledge has pointed out in his book, *Science since 1500*, have played a tremendous role in the history of science. It is also a story which demonstrates for the benefit of teachers at all levels, the vital importance of enthusiasm.

Education of today, especially at the university level, must be flexible to be fair to students who may be degree-labelled for life; they must have an opportunity to pursue that which they really wish to pursue. But to be fair to the society in which these students will have to find employment as well as to the student, it must also be broad, for despite technological advances we have a long way to go before our societies can accommodate a life of activity on a specific individual interest for each and every one of its members. The most important thing to ask of life is the opportunity to do that which one is most interested in doing; preferably to get paid for doing it but, to do it anyway. All too often, life will say no; but love will find out the way.

Brian Hocking



# THE INSECT COMMUNITY ASSOCIATED WITH ROSE GALLS OF *DIPLOLEPIS POLITA* (CYNIPIDAE, HYMENOPTERA)

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*The single chambered gall of Diplolepis polita (Ashmead) (Cynipidae) is initiated in the early spring on immature leaves of Rosa acicularis Lindl. (Rosaceae). D. polita larvae and succulent gall tissues attract five additional insect species which, by their inter-relationships within the galls constitute a community. Each species appears over a different period so that the community undergoes succession and climax. Life cycles and roles of all members of the community are discussed. Most of the D. polita larvae are replaced early in the season by larvae of the inquiline Periclistus pirata (Osten Sacken) (Cynipidae). P. pirata larvae cause additional cell proliferation and in the process of becoming enclosed in layers of cells, structurally modify their host galls. Galls inhabited by P. pirata are larger than galls inhabited by D. polita. Larvae of P. pirata are the main food source for four entomophagous inhabitants: Eurytoma longavena Bugbee (Eurytomidae), Glyphomerus stigma (Fabricius) (Torymidae), Torvus bedeguaris (Linnaeus) (Torymidae), and Habrocytus sp. (Pteromalidae).*

*La Communauté d'Insectes Associés avec des Galles de Rose de Diplolepis polita (Cynipidae, Hyménoptère)*

## Sommaire

*La galle de Diplolepis polita (Ashmead) (Cynipidae) d'une seule chambre s'initie de bonne heure le printemps sur des jeunes feuilles de Rosa acicularis Lindl. (Rosaceae). Les larves de D. polita et les tissus succulents des galles attirent cinq autres espèces d'insectes, qui par leurs relations constituent une communauté. Chaque espèce se manifeste pendant une période différente de l'année et comme résultat la communauté subit une succession d'habitants et une période d'apogée. Les cycles vitaux et les rôles de tous les membres communautaires sont analysés. La plupart des larves de D. polita s'est remplacée tôt dans la saison par des larves de Periclistus pirata (Osten Sacken) (Cynipidae). Ces larves de P. pirata évoquent une nouvelle prolifération de cellules et pendant le processus de se faire entourer par des couches cellulaires, elles font modifier la structure de la galle-hôte. Les galles habitées par P. pirata sont plus grandes que celles habitées par D. polita. Les larves de P. pirata servent de nourriture principale des quatre habitants entomophages: Eurytoma longavena Bugbee (Eurytomidae), Glyphomerus stigma (Fabricius) (Torymidae), Torvus bedeguaris (Linnaeus) (Torymidae), et Habrocytus sp. (Pteromalidae).*

Cecidology, the study of plant galls, has long been of great interest to biologists. Although galls have been mentioned in the literature since ancient times (Hippocrates, 406-377 B. C., wrote on the medicinal properties of galls) it was not until the late eighteenth century that any attempt was made to explain the connection between galls and the insects found in them. Malpighi was probably the first to explain that the stimulus for gall formation was of animal origin (Plumb, 1953). Cosens (1915) reviewed the older gall literature in a paper in which he discussed the founding of cecidology. Plumb (1953) also presented an excellent review of early cecidological literature and explained the development of theories about the source of gall forming stimuli, sites of action, and gall developmental morphology.

Although a great deal of literature on insect galls has been amassed, much of it is only systematic. Most cecidological workers in North America have occupied themselves with the classification of galls and gall insects and have disregarded fundamental problems such as gall initiation, developmental morphology, and the inter-relationships of the inhabitants composing the gall communities. Checklists are prominent in North American cecidological literature and the most popular is by Felt (1940). The most comprehensive treatise of European galls and gall formers is by Buhr (1965).

Insect galls can be defined as atypical growths produced by plants in response to a foreign stimulus. This stimulus, either chemical or physical, or both, can be provided by the larvae or the adult gall former. Gall formers are found in at least 8 insect orders, but the majority are restricted to the families Cecidomyiidae and Cynipidae. Of the approximately 1,450 gall formers in North America (Felt, 1940), about 38% belong to the order Hymenoptera. Of the hymenopterous gall formers, 91% belong to the family Cynipidae, the galls of which are recognized by all students of cecidology as the most remarkable in variety and complexity.

For gall development to occur, the life cycle of the gall former must be synchronized with the optimum galling conditions of the plant. One prime requisite for gall formation is the presence of meristematic tissue. The plant must be in such a condition that the foreign stimulus can alter normal growth patterns. Malyshev (1968) suggested that gall wasps can convert relatively differentiated tissue back into the meristematic state. Wells (1920) suggested that the gall former actually causes the dedifferentiation of host tissue, preventing the normal expression of host characters. Once dedifferentiation has occurred, stimuli from the insects cause the gall to grow into its specific shape. All galls, especially the more complex, have characteristic shapes and structures. The structure of a gall depends upon the genus of insect producing it rather than upon the plant on which it is produced. Kinsey (1920b) suggested that many gall-causing Hymenoptera may be more readily identifiable by their galls than by their own morphological characters.

Although a few gall insects are found on more than one host species, nearly all are specific to a single host genus. Cynipids have found optimal conditions on the oaks since 86% of the known species are associated with this genus. Malyshev (1968) suggested that this can be attributed to the fact that oaks are slow growing and have shoots that stay fresh and susceptible to galling for a long time. Most of the remaining cynipid species are associated with members of Rosaceae and 7% of these are restricted to the genus *Rosa*. A possible explanation for this might be Malyshev's suggestion that primitive Cynipidae caused galls on common ancestors of Rosales and Fagales and the two orders subsequently diverged.

Galls are not evenly distributed on various parts of their host plants. Besides being host specific, gall formers restrict themselves to specific plant organs. Mani (1964) reported that 5% of the known cynipid galls on *Quercus* form on the roots, 22% on branches, 2% on flowers, 4% on acorns, and about 63% on leaves. He also reported that over 80% of the galls on Rosaceae are formed on leaves.

Küster (1911) distinguished two kinds of galls on the basis of structure. He termed the more primitive galls the kataplasmas and those more complex, the prosoplasmas. Both terms have been widely used. The kataplastic galls (e.g. those caused by aphids) are characterized by a lack of both definitive tissues and constant external shape. Kataplastic galls are composed of homogeneous parenchyma cells, show little differentiation, and are structurally similar to the meristematic tissues from which they develop. Prosoplastic galls are characterized by a definitive size and form. Their tissues, differentiated into well defined zones, are fundamentally different from the normal host tissue. Most cynipid galls are prosoplastic. Wells (1921) presented evidence that prosoplastic galls were phylogenetically derived from kataplastic galls.



Gall structure depends on many factors, including time of oviposition and number of eggs laid in one area. Galls developing with one larva present are termed monothalamous and those containing several larvae are termed polythalamous. In polythalamous galls, each larva is individually surrounded by plant tissue.

Insect galls are often inhabited by numerous species besides the gall former because of the attractiveness of localized concentrations of nutritive plant tissues. The inter-relationships of insect gall inhabitants constitute one of the most important aspects of cecidology. One European gall is reported to have over 75 species of insects associated with it (Mani, 1964).

One of the first tasks in studying inter-relationships of gall insects is to determine the feeding habits of each species. Mani (1964) listed 33 different roles into which gall inhabitants can be classified. I found five insect species associated with the *Diplolepis polita* galls in my study area; they exhibit a variety of feeding habits. Both phytophagous and entomophagous species are present. The gall-forming cynipids are phytophagous for their entire larval stage. One of the inhabitants is also a phytophagous cynipid and although it is unable to initiate galls of its own, it is able to cause further proliferation of gall tissues. Galls inhabited by these insects are not only structurally modified, but also grow much larger. The four remaining species are entomophagous and feed on their hosts either as parasitoids or ectoparasites.

It must be stressed that associating entomophagous species with a particular gall does not give information on host-prey relationships. Great care must be taken in rearing experiments to determine these associations and the present study is one of few where relationships of the entomophagous species in a gall community have been determined.

Little work has been done on the biology of insect galls in Alberta. There has yet to be a checklist compiled for the galls of Alberta and Western Canada. Only the aphid galls have received concentrated attention (Harper, 1959a, 1959b, and 1966; Cumming, 1968). A.C. Kinsey, in several of his works, mentioned receiving galls from Calgary, Alberta. Weld (1926) recorded that a worker in Toronto received galls of *Diplolepis bicolor* (Harris) and *D. multispinosus* (Gillette) from Calgary.

The purpose of this paper is to examine the biology and inter-relationships of each species found in the *D. polita* gall. It is also my objective to show that the associations of species within the gall constitute a community. Each species has its role in the community and the sequence of appearance of each species initiates changes in the community's structure. Because various community attributes such as succession and climax can be examined with relative ease, studying galls may in many ways add to our general knowledge of community ecology.

All species studied in this work are new locality records for Alberta and greatly extend known distributions. Long series of all species discussed have been deposited in the Strickland Memorial Museum, University of Alberta, the University of Saskatchewan Insect Collection, and the Canadian National Collection of Insects in Ottawa.

## STUDY AREA

All field work was conducted at the George Lake Field Station of the Department of Entomology, University of Alberta, 40 miles N. W. of Edmonton, Alberta (53° 57' N, 114° 06' W). All galls used in the community inter-relationship studies were found within the one square mile field station situated on the southern margin of the boreal mixed forest subzone (LaRoi, 1968). Fire is an important feature of the boreal mixed forest subzone and has influenced the ecology of George Lake. The forest is otherwise essentially untouched, with

only some isolated logging prior to 1930. *Ledum groenlandicum* Oeder bogs and *Carex* species meadows are found in several places. There are a few open areas which allow bush stratum species to grow densely. Principal trees of the upper stratum are *Populus balsamifera* L. and *P. tremuloides* Michx. Other trees present, but less common, are *Betula papyrifera* March., *Picea glauca* Moench., *Alnus tenuifolia* Nutt., and several species of *Salix*. The bush stratum is more diverse and the dominant species are *Rosa acicularis* Lindl., *Rosa woodsii* Lindl., *Amelanchier alnifolia* Nutt., *Cornus stolonifera* Michx., *Ribes lacustre* Pers., and *Viburnum edule* Michx. Common herbs are *Epilobium angustifolium* L., *Heracleum lanatum* Michx., and several species of *Solidago*.

### GENUS *DIPLOLEPIS* GEOFFROY

Dalla Torre and Kieffer (1910) and Weld (1952b, 1957, and 1959) gave excellent descriptions of the family Cynipidae along with keys to the subfamilies and genera. A brief description of the genus *Diplolepis* was included by Dalla Torre and Kieffer. The main character used to distinguish the genus is the plowshare-shaped hypopygium. Kinsey (1920b) gave data on the phylogeny of the cynipid genera and presented biological characters of each. So far as known, *Diplolepis* species form galls only on *Rosa*.

There is considerable confusion in the literature about which generic name should be applied to cynipids forming galls on *Rosa*. *Rhodites* Hartig has been used extensively in cynipid literature, but Rohwer and Fagan (1917) established that *Diplolepis* Geoffroy had priority. Because *Rhodites* and *Diplolepis* are isogenotypic, *Rhodites* disappears in synonymy. Some Europeans still use *Rhodites* as there is sentiment for having it placed on the conservanda list, but Eady and Quinlan (1963) used *Diplolepis* in their key to the British species. Kinsey and Ayres (1922) were the first North Americans to use *Diplolepis*. When Felt (1940) republished his North American checklist of galls, he also changed to *Diplolepis*. There has also been confusion as to whether Geoffroy (1762) or Fourcroy (1785) is the author of *Diplolepis*. Weld (1952a) reviewed the nomenclature problem and recognized Geoffroy.

*Diplolepis* is Holarctic in distribution. Dalla Torre and Kieffer (1910) and Eady and Quinlan (1963) gave keys to the European species. Dalla Torre and Kieffer also included a number of North American species and provided brief descriptions of each. No inclusive key to North American species has been published. All species descriptions are brief and require extensive elaborations. Males are seldom mentioned in the literature. Undoubtedly new species remain to be described and a complete revision of the genus may show some of the existing names to be synonyms. Felt (1940) recorded 25 species of *Diplolepis*, as well as many varieties, as occurring in North America. There are now about 30 known species and two of these (*D. mayri* Schl. and *D. rosae* L.) have been introduced. Weld (1957 and 1959) listed the species found in various areas of the United States and gave brief descriptions of their galls.

#### *Diplolepis polita* Ashmead and its Gall

*Diplolepis polita* was described by Ashmead (1890) as forming galls on the leaves of *Rosa californica* Cham. and Schlecht. As with other Nearctic *Diplolepis*, the recorded description of *D. polita* is brief and inadequate. One of the key characters used to distinguish the species is its smooth and shiny mesopleura. The mesoscutum, particularly the posterior region, is not as rugose as in other species. Both Ashmead (1890) and Dalla Torre and Kieffer (1910) stated that males and females are entirely black. All females from George Lake have a reddish-brown abdomen as well as reddish-brown legs.

*D. polita* has been found only in North America. Ashmead (1890) examined specimens from California, Dakota, and Colorado. Weld (1957) recorded *polita* as being found on the Pacific coast but did not mention it (1959) as occurring in Eastern United States. *D. polita* is not mentioned in Eastern North America checklists. Galls of *D. polita* were the most common of the *Diplolepis* galls found at George Lake in 1968 and 1969. I have collected specimens throughout Alberta, but it appears to be most common in central and northern regions. The previous most northern locality recorded was Ashland, Oregon (Bugbee, 1951).

Ashmead (1890) mentioned receiving galls of *D. polita* from Cockerell who had used the manuscript name *spinosellus*. Cockerell (1890) stated that *D. spinosellus* was a new species, but gave no description of the gall former or the gall. Muesebeck *et al.* (1951) declared *spinosellus* Cockerell invalid. Krombein and Burks (1967) again used the name but gave no reference to descriptions of the gall former or the gall. Fullaway (1911) also made brief mention of *D. polita* and its gall. According to Weld (1952a) Fullaway misidentified the *polita* adults and instead considered them *D. bicolor*. Weld examined Fullaway's specimens and found those labelled *D. bicolor* were actually *D. polita*. Beutenmuller (1922) also obtained some of Fullaway's specimens described as *D. bicolor* and realizing they were not *D. bicolor*, proposed the name *D. occidentalis*. Weld (1952a) examined Beutenmuller's *occidentalis* and confirmed its synonymy with *polita*.

The gall of *D. polita* is small (average diameter 4.0 mm), spherical, monothalamous, and is spinulose and sometimes tuberculose. All galls collected were found on the adaxial surface of the leaflets (Figs. 1 and 2), although McCracken and Egbert (1922) stated that they can also be formed on stems. McCracken and Egbert also stated that the gall varies in size from 5 to 10 mm in diameter and often harbours inquilines. Their measurements were probably from inquiline modified galls rather than unmodified *D. polita* galls. *D. polita* galls are usually found in clusters, several galls per leaflet (Fig. 2), although individual galls on a leaf have been found. The largest number of galls found on one leaf was 39. Of all the galled leaves collected, 61% were host to 5 galls or fewer. Galls growing close to one another often coalesce.

Immature galls (Fig. 1) are often smooth or with weakly developed spines. They are soft and composed of large succulent cells, many of which are visible to the naked eye. The *polita* larva is tightly nestled in the interior of the gall where it feeds on the rapidly growing cells. Cells next to the larva often appear much larger than other cells of the gall wall and it is presumed that they play an important role in the larva's nutrition. As the gall matures the walls become brittle and the spines more conspicuous. The spines are easily broken off and as a result galls handled in the laboratory for some time may appear spineless (Figs. 3-6). The mature gall is hollow and smooth on the interior and the last instar larva has an increased amount of space inside the gall (Fig. 3).

Nothing has previously been recorded on the anatomy of the gall other than brief comments. Beutenmuller (1907) mentioned that the gall is thin walled and hollow. McCracken and Egbert (1922) were the first to establish that the gall is monothalamous. My histological studies (Ms. in preparation) show the gall to be prosoplasmic for the wall tissue is composed of four well defined zones.

Two temporally separated groups of *D. polita* galls appeared at George Lake in both 1968 and 1969 seasons. Most galls appeared in the early spring on mature rose plants and in this study are referred to as spring initiated galls. The second group of galls appeared later in the season on new sucker shoots and are referred to here as sucker shoot galls. Sucker shoot galls are somewhat different in appearance from spring initiated galls, often more densely covered with long and hair-like spines. Although sucker shoots probably begin growth in the



Fig. 1. Immature gall of *Diplolepis polita* on leaflet of *Rosa acicularis* Lindl. George Lake, Alberta. May 20, 1969. Fig. 2. Mature galls of *Diplolepis polita*. George Lake, Alberta. August 10, 1969.

spring, they were first observed near the end of June in both seasons. Sucker shoots are sterile and have larger and more succulent leaves than do older plants. They grow rapidly and most attain a height of 0.9m by the season's end. Their stems are densely spined and the tall thin plants produce few side branches. New sucker shoots were more common around open areas such as *Ledum* bogs and artificial clearings than in the forest.

It has been recorded by several authors that galls growing under various physiological conditions differ in their colorations. Both greenish-yellow and red galls of *D. polita* were found and the amount of sunlight received by the host plant appears to regulate colour. Cosens (1912) stated that galls of *Pontania pomum* Walsh (Family Tenthredinidae) are poorly colored if they grow in deeply shaded areas. *D. polita* galls growing in the shade of *Populus* species are generally a light greenish-yellow. Galls on plants growing in open spaces such as meadows, roadsides, and burned over areas are often bright red, especially when immature. Galls appearing on sucker shoots and those growing in darkly shaded areas may be creamy to pure white in color. Niblett (1943) noted this for the galls of *D. eglanteriae* Htg. and *D. rosarum* Gir. As the *D. polita* galls mature they become brown.

Schröder (1967) found that galls of *D. rosae* were more numerous on roses growing under stress. He reported that plants suffering from a lack of water supported more galls. These plants were small, their yearly growth poor, foliage thin, leaves smaller than normal, and often pale in color. They are unlikely to be the sucker shoot plants described in this paper. Schröder found these plants growing in areas subjected to extreme insolation and although they were common, their growth was poor. He observed ovipositions in both vigorous and weak plants and found that no galls formed on the vigorous plants. He suggested that the osmotic pressure of vigorously growing plants may be responsible for fewer galls. The rarity of *D. rosae* galls on domestic roses also indicates that healthy plants are able to suppress gall formation. *D. polita* galls appeared no more common on plants growing in open spaces such as roadsides than they did on plants growing in shaded areas. Galls occurring in such areas were, however, found to be much more brittle than galls growing in shaded areas.

In any study concerned with insect galls, it is vital that careful attention be paid to the accurate identification of host plants. Although *Diplolepis* species are restricted to *Rosa*, several species can form galls on more than one host species. Niblett (1943) recorded *D. eglanteria* on 7 species of rose. Harrison (1922) exposed 16 species of rose to *D. rosae* and found that oviposition took place only on members of one section. The 3 species of rose found in Alberta are *R. acicularis* Lindl., *R. woodsii* Lindl., and *R. arkansana* Porter, all belonging to section Cinnamomeae. Lewis (1957) emphasized that the genus *Rosa* is one of the most difficult groups to separate into distinct species. Species hybridize with ease giving fertile offspring and the wide variation contributes to identification problems. Of the two species found at George Lake *R. acicularis* is more common than *R. woodsii* and is generally taller, less bushy, and has larger leaflets. *R. woodsii* flowers later in the season and usually has more densely spined stems (both species determined by W. H. Lewis). Galls of *D. polita* were found only on *R. acicularis* at George Lake. Lewis (1959) illustrated the Holarctic and Nearctic distribution of *R. acicularis* and stated that it has the most extended native range of any species in the genus. *R. acicularis* is native to Northern Europe, Asia, and North America.

### The *Diplolepis polita* Gall Community

I define an insect gall community as the assemblage of insect populations associated with a collection of galls initiated by the same species of gall former. For the purpose of this paper, the assemblage of insects obtained by making large random collections of galls within

the study area, was considered to constitute the *Diplolepis polita* gall community. Mani (1964) defined climax of gall community succession as being marked by a dominance of entomophagous species. Climax in the *D. polita* gall community can also be defined as being reached when the galls mature and fall to the ground, for once this stage is reached, oviposition and larval feeding activities cease. The periods of emergence and oviposition for all species in the community occur in sequence. Emergence early or late in the season would reduce the reproductive success of that species.

The present study investigates five species found associated with the larvae and galls of *D. polita*. These are *Periclistus pirata* (O.S.) (Cynipidae), *Eurytoma longavena* Bugbee (Eurytomidae), *Glyphomerus stigma* (Fabricius) and *Torymus bedeguaris* (Linnaeus) (Torymidae), and *Habrocytus* sp. (Pteromalidae). Incidentals found associated with a very small percentage of galls were *Eupelmella vesicularis* Retz (Eupelmidae), *Ormyrus* sp. (Ormyridae), and *Tetrastichus rosae* Ashmead (Eulophidae).

Gall inhabitants that feed on gall tissues and do not directly attack the gall former have been termed inquilines. The term inquiline is derived from the Latin 'inquilinus' meaning tenant or guest. According to Askew (1971), inquilinism is a form of commensalism, somewhere between parasitism and symbiosis. An inquiline lives in close spatial relationship with its host, not feeding upon the host, but nevertheless frequently destroying it. In a commensal association all the advantages are to one of the partners and it is common that some commensals do more harm to their hosts than depriving them of some larval food. Though some workers have used inquiline in a somewhat different or broader sense (Triggerson (1914), Malyshev (1968), Lyon (1969)), Askew's definition seems most appropriate.

A close taxonomic relationship between the commensal and its host often exists in inquilinism. Muesebeck et al. (1951) listed the inquiline species of *Periclistus*, *Ceroptres*, *Synergus*, and *Euceroptres* as being guests in insect galls, all being of the family Cynipidae. All species of *Periclistus* are restricted as inquilines of rose gall wasps as are *Synergus* of oak gall wasps. It is probably safe to assume that inquiline cynipids had an ancestor capable of inducing galls. This is indicated by the retention of the ability to induce cell proliferation in many species such as *P. pirata*. Askew (1971) has suggested that inquilinism is on the road to parasitism, demanding only that the inquiline become entomophagous rather than phytophagous.

Some oak galls are inhabited by inquilines that do not interfere with the gall former. Instead they form irregular chambers inside the thick walls of their host gall (Sternlicht, 1968) and do not come in contact with the gall forming larvae. Other oak gall inquilines occupy the central chamber of the gall former (Askew, 1971). Inquilines such as *Periclistus* and *Synergus* species initiate chambers of their own inside galls and in the process obliterate the chamber of the gall former. These species are incapable of initiating gall formation and are completely dependent upon the gall formers for the provision of their larval food.

Osten Sacken (1865) was one of the first to question the inquiline behavior of *Periclistus* species. *Periclistus pirata* was found in nearly all *D. polita* galls and all such galls were modified by the *P. pirata* larvae forming individual chambers. Because *P. pirata* does not feed upon tissues of *D. polita*, it cannot be described as a parasite or predator but instead fits Askew's definition. No galls inhabited by *P. pirata* contained the larva of *D. polita*. It is suggested that the *D. polita* larva is killed when the *P. pirata* oviposits in the immature galls.

There is little uniformity in the literature as to usage of terms associated with entomophagous species inhabiting galls. Common terms such as parasite and predator are often misused. Smith (1916) distinguished parasites and predators on the number of hosts required to complete development. He defined parasitic insects as those which pass their entire larval

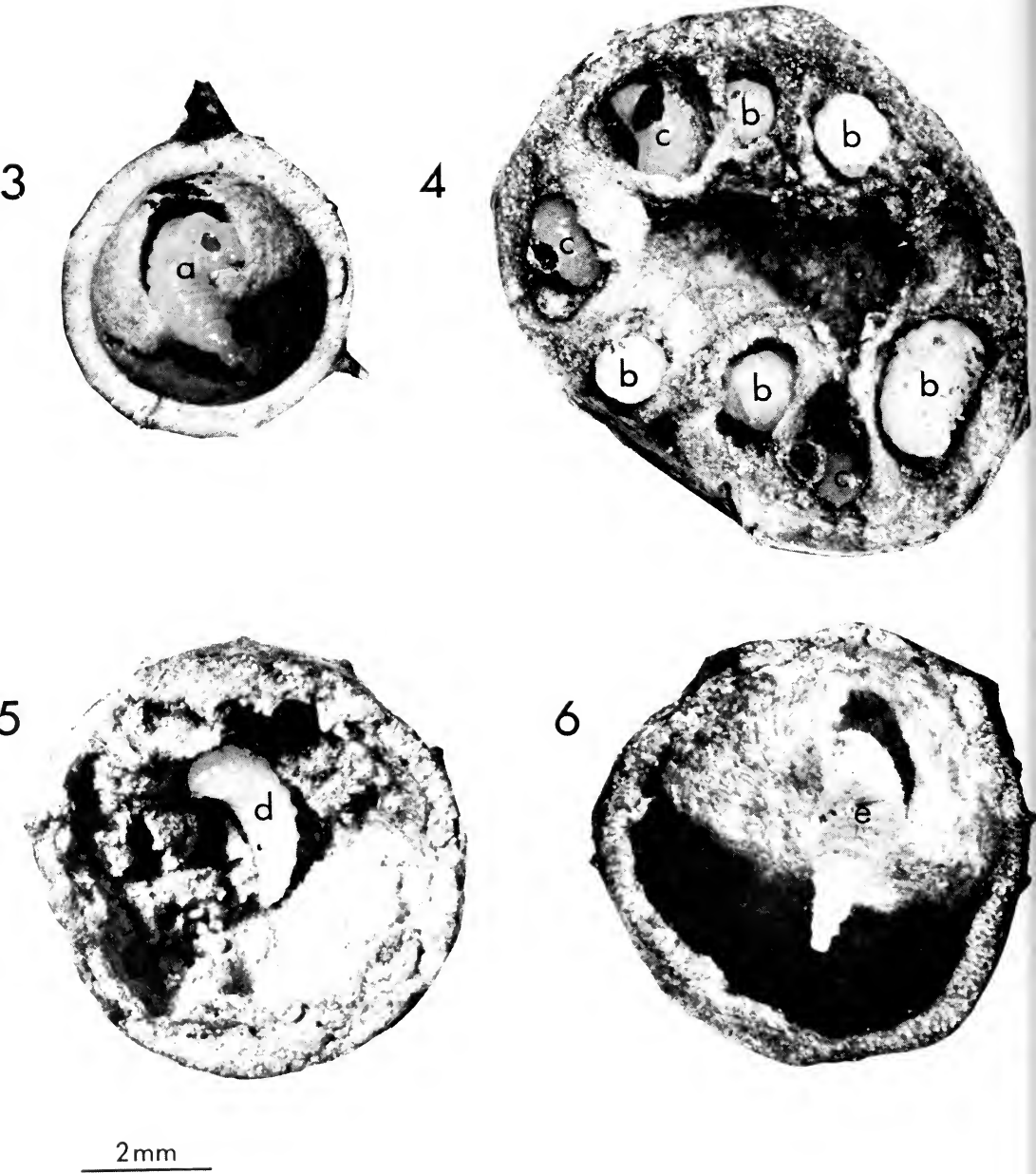
stage within or upon a single host and predacious insects as those which require more than one host to complete development. He also noted that a distinction between parasitism and predation is of limited importance and it is wise to keep in mind that many species are called parasites only because they belong to parasitic groups and not by reason of their behaviour. Many students of galls use the term predator only when referring to birds or mammals which break into galls. There is also a common feeding habit of entomophagous insects intermediate between parasites and predators for which the term parasitoid has been introduced. Parasitoid has been suggested for those insects which destroy their hosts (which are usually insects), are of a relatively large size compared with their hosts, and are parasitic as larvae only (Doutt, 1959). It has not been widely accepted although has received some usage in major works such as Askew, (1971). Its use has merit in gall studies because many of the inhabitants are not true parasites nor can they be considered typical predators. Doutt (1964) discussed the system for classifying entomophagous insects based on host relationships. Parasites attacking a phytophagous host are termed primary parasites. If the primary parasite is attacked, then its enemies are called secondary parasites.

*Eurytoma longavena*, a common inhabitant of the *D. polita* gall, chews its way from chamber to chamber often consuming two or more *P. pirata* during its development. *Glyphomerus stigma* and *Torymus bedeguaris* may feed ectoparasitically or as parasitoids. Blair (1944) described *G. stigma* and a *Torymus* as ectoparasites. *Habrocytus* sp. was found feeding only on individual larvae of *P. pirata*, that is, as an ectoparasite. Before examining the community inter-relationships of the *D. polita* gall, it is first necessary to examine the biology of each inhabitant species.

## METHODS

Galls collected in both 1968 and 1969 were used for studying life cycles and the roles played by each species in the community. Most of the galls collected in 1968 were used for associating larvae of the inhabitants with their adults and studying life cycles of each. Galls collected throughout the season were dissected to obtain larvae and determine their feeding behavior. Most larvae were readily distinguished morphologically (Figs. 7-12) and for three species, *P. pirata*, *E. longavena*, and *G. stigma*, the larvae were also identifiable by examining the characteristic damage done to the gall tissues (Figs. 3-6). Eggs of only *P. pirata*, *E. longavena*, and *G. stigma* were easily identified. When mature larvae were found, they were placed in small pin-mounted gelatin capsules as described by Shorthouse (1972). Large numbers of larvae were stored in standard insect specimen boxes where they could be checked for developmental changes. These specimen boxes were stored in a field laboratory under nearly ambient conditions of temperature and humidity to obtain fall emergents. The remaining larvae were then returned to the university, stored at 4°C for 3 months, then incubated at room temperature (approximately 22°C) when a 65% emergence was obtained. Once the larvae pupated, the mandibles were removed from the larval cast skins and mounted on slides. Mandibles of the larvae are structurally dissimilar (Figs. 13-18) and useful for identifications. A correlation among adult, larva, larval mandibles, and feeding behavior was obtained in this manner for each species. Other collections of mature galls made in the fall of 1968 were stored undissected in plastic vials. Fall emergents were removed as they appeared and the galls then subjected to 4°C to break diapause.

Galls collected in the 1969 season were used for observing seasonal changes in the community composition. A total of 27 collections were made. Each collection was made by randomly walking through areas of rose and collecting every gall observed. These walks were



Figs. 3-6. Mature *Diptolepis polita* galls. 3. Gall inhabited by *Diptolepis polita*. 4. Gall modified by *Periclistus pirata*. 5. Gall modified by *Eurytoma longavena*. 6. Gall modified by *Glyphomerus stigma*. (a) *Diptolepis polita* larva; (b) *Periclistus pirata* larva; (c) *Habrocytus* sp. larva; (d) *Eurytoma longavena* larva; (e) *Glyphomerus stigma* larva.



often more than 1,000 metres in length with the result that each collection was composed of samples from numerous rose patches throughout the study area. When a gall or gall-cluster was found, the entire leaf was picked and placed into an 18 ounce 'Whirl-Pak' bag. Size of each collection was roughly governed in the field by collecting two bagfuls of galled leaves. Only 11 of the 27 collections were used for the community study. The first 3 collections were small because of the scarcity of galls in the early spring, but from June 6 until the end of August, galls were sufficiently common that the two bags could be filled within two hours. Because nearly all galls had matured by August 8 (Fig. 28), only one large collection was used for August. Approximately 4,500 galls were collected in this manner. All galls were returned to the laboratory, measured, dissected, and the contents examined, or the galls were fixed in FAA solutions for later examination.

In this study, an empty gall is defined as one which does not contain a live inhabitant and therefore cannot contribute to the community. Galls from which *E. longavena* or *T. bedeguaris* emerged late in the season each had a tiny emergence hole and were considered separately.

### LIFE CYCLES OF GALL INHABITANTS

#### *Diplolepis polita* (Ashmead)

Few data have been published on the biology of North American *Diplolepis* species and nothing has previously been published on the biology of *Diplolepis polita*. Most North American publications such as Bassett (1890), Beutenmuller (1907), Kinsey and Ayres (1922), McCracken and Egbert (1922), Osten Sacken (1863, 1865) and Weld (1926, 1952a, 1952b, 1957, and 1959) are concerned mainly with species descriptions. Europeans and Asians have contributed much more to our knowledge of *Diplolepis* biology; notable examples being Blair (1944, 1945a), Callan (1940), Kuznetsov-Ugamskij (1930), Niblett (1943, 1947), Schröder (1967), and Yasumatsu and Taketani (1967).

Only 21 adults of *D. polita* were obtained throughout the study. All were reared from galls stored in the laboratory. No adults were collected by sweeping or trapping in 1968 or 1969, nor were any adults observed ovipositing. No adults of other *Diplolepis* species were collected in the study area either and it is assumed that field work began too late in the season. The earliest search for adults began May 7, 1969. Schröder (1967), in his study of *D. rosae* (L.), found that emergence occurred over a period of from 2 to 6 weeks, extending to 8 weeks if the weather was cool. He found that more individuals emerged on warm sunny days than on cool rainy days. He also observed that some females were able to pass a number of days at temperatures below the freezing point without harm. However, Kinsey (1920a) found that most adult cynipids are killed by sudden changes of temperature or humidity and that adults emerging during inclement weather would not oviposit. Niblett (1947) suggested that late frosts are responsible for many casualties and in years when these frosts occur, few galls are to be found. There may be inter-specific as well as generic differences in tolerance of inclement weather conditions.

Yasumatsu and Taketani (1967) observed and described the oviposition of *D. japonica* (Walker) and estimated the time required for initial gall growth to occur after oviposition. It is well established (Mani, 1964) that gall formation is due to larval feeding and if proliferation begins soon after the larva commences feeding, the period between oviposition and hatching can be estimated. Yasumatsu and Taketani estimated that the egg stage of *D. japonica* lasts from 7 to 10 days. Callan (1940) experimented with *D. rosae* and found that the first sign of gall formation was from 12 to 36 days after oviposition. Schröder (1967),

studying the galls of the same species found hatching about 7 days after oviposition and that the gall begins to grow 4 to 5 days later. I found the first *D. polita* galls May 20, 1969 so probably oviposition occurred before May 10 in 1969 and as a result the first visible growth occurred between May 20 and 25. Since no adults were collected when the field search began on May 7, *D. polita* emergence and oviposition probably takes place in late April or early May. Alder and Straton (1894) suggested that adult life is shorter in species of gall wasps which deposited eggs over a short period. *D. polita* adults lived for an average of 4 days in the laboratory which suggests that their eggs are deposited over a short period of time. Kinsey (1920a) found that *Diplolepis* adults live for only a few days and must oviposit soon after emergence.

The eggs of *D. polita* are probably laid in or on the leaf primordia of slightly forced *R. acicularis* buds. Schröder (1967) found that the eggs of *D. rosae* were deposited on the median vein of the pinnules as well as on the developing petioles. He found that the anterior ends of the eggs are inserted into the epidermis of the developing leaflets, leaving the greater part of the egg free between the folded leaves. A similar situation probably occurs with *D. polita*. The eggs of *D. polita* are similar to the stalked eggs of other cynipids described by Berland (1951). *D. polita* females must contain a large number of eggs for although their population is low in the spring (Fig. 21), their galls were one of the most common in the study area. Yasumatsu and Taketani (1967) found that *D. japonica* females contained an average of 331 eggs whereas Schröder (1967) found that 5 to 7 day old *D. rosae* females contained an average of about 780 eggs.

As with all *Diplolepis* species the larvae feed on host tissues and initiate formation of the gall. Little data could be obtained on the time required to complete larval development since this and the time of oviposition depend on factors such as condition of the host plant, which undoubtedly differs from area to area. Hence periodic collections do not clearly indicate the succession of larval instars. *D. polita* larvae have 12 body segments (Fig. 7), lack setae, and undergo an estimated 5 larval instars. Mandibles of the last instar larva are tridentate (Fig. 13). The larvae grow rapidly and continue feeding on succulent gall cells until the gall matures and hardens. Cosens (1912) stated that cynipid larvae feed only on cell contents resulting in the occurrence of collapsed cells around the larva. No fecal material is found inside the gall for the larval gut is blind. When the leaf tissue surrounding the gall matures, the galls fall to the ground where they are protected by snow through the winter. All *Diplolepis* species overwinter as mature larvae. Laboratory reared specimens had a short pupal stage lasting on the average about 10 days. Adults emerge inside the gall and must chew their way through the wall to escape.

When the *D. polita* adults emerge in the early spring, it is assumed that they immediately begin searching for oviposition sites. Callan (1940) found that most males of *D. rosae* appeared before the peak appearance of females. It is well established that parthenogenesis occurs throughout the genus and that males are rare, if found at all. Callan also suggested that some species may exhibit geographic parthenogenesis, that is, males may be more numerous in northern populations. Sex ratio of the 21 specimens I obtained was 0.714 (sex ratio = number of females/ total number of individuals). Kuznetsov-Ugamskij (1930) recorded a *Diplolepis* species from Asia with a sex ratio near 0.500 and in this species parthenogenesis probably does not occur. Although most populations of *D. polita* may be parthenogenetic, the occurrence of a comparatively high number of males indicates that some sexual reproduction occurs. Kinsey (1920a) suggested that in some primitive *Diplolepis* species, normal sexual reproduction may take place, but in the genus as a whole, the male is gradually disappearing and parthenogenesis is becoming the sole means of reproduction. The presence of

males in all collections of *Diplolepis* species found in central Alberta is consistent with the geographic distribution of parthenogenesis as found by Callan (1940) and Schröder (1967).

### *Periclistus pirata* (Osten Sacken)

The genus *Periclistus* Foerster consists of 7 North American species considered by most authors (Muesebeck et al., 1951) to be restricted to an inquiline habit in the galls of *Diplolepis* species. Although the exact relationship between *Periclistus* species and the gall formers are not known, it is accepted that the livelihood of *Periclistus* species depends on the presence of *Diplolepis* galls. *Periclistus* larvae are phytophagous and feed on the same gall tissue as do the gall formers; they cannot initiate galls. There have been no studies concerned with specificity of *Periclistus* species for *Diplolepis* galls. Fullaway (1911) recorded *P. piceus* Fullaway and *P. californicus* Ashmead from galls of *D. polita*. Osten Sacken (1863) described *P. pirata* and obtained the specimens from galls of *D. ignota* (O.S.). This present study is the first record of *P. pirata* from the gall of *D. polita*.

*P. pirata* was an important occupant of the *D. polita* galls of George Lake in 1968 and 1969. Of the spring initiated galls 88.5% collected June 6, 1969 contained either eggs or larvae of *P. pirata* (Fig. 21). Blair (1944) found that *Periclistus* sp. were present in nearly all the *D. rosae* galls he examined. Although *P. pirata* larvae are phytophagous, in all galls examined in which they were present, the *D. polita* larvae had been destroyed. Fig. 21 shows that as the eggs of *P. pirata* become more abundant in gall collections, the number of galls containing a live *D. polita* larva was reduced. Although the exact mechanism of this replacement is not known, it has been recorded in other *Diplolepis* galls (Blair, 1945a). Because the *D. polita* larva was always found dead in galls containing *P. pirata* eggs, oviposition by *P. pirata* females must kill the immature *D. polita*. Once the *D. polita* larva has been killed, it shrivels and becomes difficult to detect.

*P. pirata* adults emerged early in the spring, probably two or three weeks after the *D. polita* adults had emerged and oviposited (Fig. 19). The emergence of *P. pirata* is synchronized with the appearance of the immature *D. polita* galls. Male *P. pirata* emerged before the females (Fig. 20). The first males were collected in the field May 16, 1969 the first females May 20, 1969, and the first oviposition was observed May 23, 1969. By June 1, 1969, adults of *P. pirata* were common and 263 were obtained by hand collecting. In the evening the adults rested under the upper leaves of *Rosa* and could be easily dropped into collecting vials. Sex ratio of the adults collected in this manner and from spring rearing experiments was 0.557. It is interesting that an inquiline cynipid species should have a population composed equally of the sexes whereas the gall former populations are dominated by females. Copulation was observed on many occasions both in the field and in the laboratory and it is therefore doubtful that parthenogenesis occurs. Over 300 observations of *P. pirata* ovipositing in immature *D. polita* galls were made (see feature photograph, Ent. Soc. Can. Bull., 1970.2 (4): 102). If both immature and mature galls were present in a cluster, the immature galls would always be chosen for oviposition first. *P. pirata* must have a lengthy emergence period for although most of the population emerges in the spring, adults were found ovipositing in galls up to August 7, 1969. The reappearance of immature galls in July of 1969 (Fig. 25) allowed late emerging females the opportunity for oviposition. The July increase in the number of galls containing *P. pirata* eggs (Fig. 21) is due to the appearance of sucker shoot galls. The mean number of eggs per gall for all collections is given in Table 1. *P. pirata* females oviposited readily in galls that contained eggs from other females. The largest number of eggs found in a spring initiated gall was 23, largest number in a sucker shoot gall 16. This may be

because more *P. pirata* females were present in the spring. The ease with which oviposition could be induced in the laboratory and the observations of oviposition during rainy cool weather, indicated that this species is much more hardy than *Diplolepis* species.

The egg of *P. pirata* is white, of the hymenopteriform type (Clausen, 1940), banana-shaped, and stalked. The stalk, which is as long as the egg, is elastic and has a slight bulge at the distal end. Upon hatching, the larvae distribute themselves around the inner walls of the gall and commence feeding on gall tissues. *P. pirata* larvae initially feed on the same cells as *D. polita* larvae and the area in which they feed is always marked by a layer of empty cells. As the larvae continue feeding, gall tissue surrounds each individual to form an inner chamber (Fig. 4). Blair (1945b) found that *Synergus reinhardi* Mayr (Cynipidae) modified the galls of *Cynips kollari* Hartig (Cynipidae) in a similar manner. Galls containing *P. pirata* chambers appear polythalamous and the original cavity, once containing a single *D. polita* larva, is nearly obliterated (Fig. 4). *P. pirata* larvae (Fig. 8) are easily distinguished from those of *D. polita* by the mandibles (Fig. 14). *P. pirata* larvae are not as active as *D. polita* larvae and do not thrash as violently when disturbed. *P. pirata* inhabited galls fall to the ground and receive the same winter protection under the snow. The seasonal change in the percentage of galls with larvae and the mean number of larvae per gall is shown in Table 1. The pupal stage of laboratory reared specimens lasted about 9 days. Many of the galls collected in the fall of 1969 which overwintered in the laboratory at 4°C and were then moved to 25°C were dissected 4 months after emergence had ceased. About 3% of the *P. pirata* inner chambers contained live larvae. Under normal conditions these larvae may have been destined for emergence later in the season or their presence may indicate that a small percentage of the *P. pirata* population remains in the larval stage throughout the season and emerges the following year.

### *Eurytoma longavena* Bugbee

Eurytomids are one of the most common entomophagous groups associated with *Diplolepis* galls. Bugbee (1967) listed 82 species of North American *Eurytoma* and stated that 33 species attack Hymenoptera. He stated that at least 12 species are known to be phytophagous and listed one species, *E. pachyneuron* Girault, suspected of being both parasitic and phytophagous. Peck (1963) presented a comprehensive bibliography for 72 North American species. Although most gall inhabiting eurytomids are considered parasitic, the lack of detailed life cycle studies hinders such generalizations. Bugbee (1951) discussed 12 species known from *Diplolepis* galls and warned that knowing the associated gall gives little data on actual host relationships. Also in this paper he discussed the phylogeny of the *Eurytoma* species associated with *Diplolepis* galls. He suggested that most *Eurytoma* are restricted to a single species of gall former, but also listed several species known from more than one gall and suggested that further studies will reveal more complex relationships. He pointed out that some species may attack inquiline and other gall inhabitants besides the gall former. Bugbee (1951) also stated that no complete life-histories have been worked out for any of the Nearctic species associated with *Diplolepis* galls.

*E. longavena* was the most common and influential entomophagous occupant in the 1968 and 1969 *D. polita* gall community. This species was described by Bugbee in 1951 and was found inhabiting *D. bicolor* galls growing on an undetermined species of *Rosa*. *E. longavena* is known only from its type locality of Terrace, British Columbia and according to Bugbee (pers. comm.) nothing is known of its biology. Three species of *Eurytoma* have previously been associated with *D. polita* galls (Bugbee, 1951); these are *E. flavicurensa* Bugbee, *E. incerta* Fullaway, and *E. terrea* Bugbee. *E. longavena* has not been previously recorded from the *D. polita* gall.

Table 1. Incidence of *Periclistus pirata* eggs and larvae in the galls of *Diplolepis polita*. George Lake, Alberta, 1969.

Date	Sample size	% of galls with eggs	Mean no. of eggs per gall $\pm$ S.D.*		% of galls with larvae	Mean no. of larvae per gall $\pm$ S.D.*	
20-V	4	0	0		0	0	
25-V	55	38.1	6.2	3.9	0	0	
28-V	54	83.5	10.1	6.8	0	0	
6-VI	166	43.6	5.4	4.8	71.0	6.9	5.5
12-VI	156	13.0	3.0	1.8	62.3	5.7	3.7
20-VI	176	8.1	2.5	1.5	37.0	4.1	3.6
27-VI	127	2.1	—		35.4	4.2	3.8
5-VII	119	0	0		25.2	3.6	3.3
14-VII	156	0	0		20.0	3.7	2.9
spring							
14-VII	21	80.9	5.0	4.1	9.5	5.0	4.1
sucker							
23-VII	190	0	0		17.2	3.9	3.6
spring							
23-VII	106	9.4	4.9	4.1	50.0	5.2	4.2
sucker							
22-VIII	275	0	0		8.1	3.5	3.2

\*means are calculated exclusive of galls without eggs or larvae

spring = galls initiated in the spring only

sucker = galls initiated on sucker shoots only

Larvae of *E. longavena* were found in 17% of the mature galls collected August 17-23, 1968 and in 32% of the galls collected August 22, 1969 (Fig. 21). Most of the empty galls found in 1968 and 1969 were also a result of *E. longavena* activities. Gall collections described under methods were used in tabulating incidence of *E. longavena* eggs, larvae, and pupae in the galls of the 1969 season (Table 2). *E. longavena* has two generations per year in the study area, although only a small percentage of the total population is derived from the second generation. From a large collection of 1969 spring initiated galls, 12.3% of the *E. longavena* population emerged the same season and the remainder emerged the following spring. Adults that emerged in the fall of the same season were able to oviposit in sucker shoot galls. The *E. longavena* population found in sucker shoot galls emerges the following spring. Clausen (1940) stated that the number of generations of *Eurytoma* per year is dependent upon the hosts attacked and mentioned that *E. monemae* Ruschka may have three generations per year.

Bugbee (1951) stated that the sex ratios for several species he studied were approximately equal although females are usually more numerous. A total of 423 *E. longavena* adults were

obtained in this study and the sex ratio was 0.912. The fall populations of *E. longavena* consisted of females only and the sex ratio of all individuals collected, exclusive of fall emergents, was 0.892. Niblett (1947) found that a small percentage of the *E. rosae* Nees populations emerged in the first year and that the sexes were in equal numbers. *E. longavena* females emerged late in the season from 5% of the mature galls collected in 1968 and from 7% of the mature galls in 1969.

Fig. 20 indicates that *E. longavena* adults begin to emerge about the same time as *P. pirata* and are probably present when the first *D. polita* galls appear. The first eggs were found in galls collected May 25, 1969, although the earliest of 53 ovipositions observed in 1969 was June 5, 1969 (Fig. 19). Spring adults emerge over a long period of time as indicated in Fig. 20, and may overlap the fall population. The last ovipositing female observed, August 9, 1969, thus may have been from either the spring or fall population. This extended activity period is also shown by the presence of eggs in sucker shoot galls (Table 2). These eggs could have been deposited by either late spring emergents or fall emergents. The mean number of eggs laid per gall is also shown in Table 2. Dates without data were due to difficulties in locating eggs amongst *P. pirata* chambers and uneaten gall tissues. As with *P. pirata*, *E. longavena* would readily oviposit in galls containing eggs from previous females.

*E. longavena* eggs are similar in appearance to other *Eurytoma* eggs described by Clausen (1940) and Phillips (1927). They are brown and have a small curled stalk at one end. The stalk is about one-third as long as the egg. The eggs are white immediately after oviposition but turn brown within 24 hours. Several *E. longavena* females were dissected and all contained 6 eggs or less. The largest number of eggs found in a spring initiated gall was 11 and the largest number in a sucker shoot gall was 4. *E. longavena* eggs were found only in immature galls containing eggs or larvae of *P. pirata*. No eggs were found in galls containing a *D. polita* larva, which indicates that the females can distinguish gall contents. Eggs were deposited along the inner walls of the gall and upon hatching the larvae immediately began feeding on the eggs or larvae of *P. pirata* and later fed on any gall inhabitants they encountered. Because *P. pirata* was the most abundant species in the gall community, it was the chief host of *E. longavena*. I observed several *E. longavena* larvae feeding even before they were completely free of their egg shells. Later in the season *E. longavena* larvae were also found consuming immature larvae of *Glyphomerus stigma*, *Torymus bedeguaris*, and *Lebrocytus* sp. *E. longavena* are also cannibalistic and though most galls attacked by this species contained several eggs (Table 2), only one larva usually survived. Of the galls containing *E. longavena* 94% produced a single adult. Galls producing two adults were large. Caltagirone (1964) stated that when more than two *Eurytoma* sp. eggs were present in the *Pontania* gall he studied, the larva that hatched first killed the remaining eggs.

*E. longavena* larvae are both entomophagous and phytophagous but they must feed on insect tissue before they feed on plant tissue. This is shown by the fact that larvae often do not survive if hatched in galls with completed *P. pirata* chambers. *E. longavena* larvae must consume free host material before they are capable of chewing through chamber walls. Once the larvae have reached a certain stage in their development, they are capable of feeding on either plant tissues or insect tissues found inside the *P. pirata* chambers. Once the *P. pirata* larvae are enclosed by gall tissues, the *E. longavena* larvae must chew through chamber walls if more insect tissue is required. If the combined feeding activities of several *E. longavena* larvae consume all insect host material before they are capable of phytophagous feeding, all will perish and an empty gall results. Most galls contained sufficient immature *P. pirata* to supply the *E. longavena* with food and also allow some *P. pirata* to escape and form chambers. It is pertinent that the hosts are not killed at the time of oviposition, for the presence

of *P. pirata* larvae provide the *E. longavena* larvae with access to succulent parenchyma cells and to other entomophagous species attracted to the chambers. Moser (1965), Caltagirone (1964), and Malyshev (1968) reported that the gall inhabiting *Eurytoma* they studied stung and paralysed the hosts at the time of oviposition. Blair (1944 and 1945a) suggested that *E. rosae* found in galls of *D. rosae* were predators, but Niblett (1947) and Askew (1961) disagreed.

When *E. longavena* larvae chew from chamber to chamber, uneaten plant tissues accumulate inside the gall and this condition is characteristic of *Eurytoma* damage (Fig. 5). Although the presence of this tissue suggests that the larvae tear through chamber walls, I observed many individuals ingesting plant cells, thus confirming that the species is phytophagous. Varley (1937) recorded the same behavior for the larvae of *E. robusta* Mayr. Blair (1954a) stated that the larvae of *E. rosae* feed on *Periclistus* larvae and chew into gall tissues but did not record a phytophagous habit. Malyshev (1968) listed several other eurytomids that initially feed on eggs and host larvae and then feed on gall tissues. It appears that once a *E. longavena* larva consumes a certain amount of entomophagous material, it is capable of continued development on gall tissues. Phillips (1927) in his study of *E. parva* (Girault), suggested that this species, similar to *E. longavena*, is gradually breaking away from the entomophagous habit and is becoming phytophagous. Blair (1945a) suggested the same for *E. rosae*.

Mature *E. longavena* larvae are recognized by their distinct segmentation, abdominal protrusions, and anterior sensory setae (Fig. 9). The larval mandibles (Fig. 15) are heavily sclerotized, triangular in outline, and each has one large denticle on the inner margin. *E. longavena* larvae, except for the fall emergents, overwinter inside the gall and pupate the following spring. The pupal stage of laboratory reared specimens lasted about 12 days.

### *Glyphomerus stigma* (Fabricius)

The genus *Glyphomerus* is monobasic containing the single species *G. stigma*. This species, described in 1793 by Fabricius, has a Holarctic distribution and is known mainly as an ectoparasite of gall inhabitants. Viereck (1916) recorded it from the gall of *D. rosae* and Hoffmeyer (1930) from the gall of *D. polita*. Peck (1963) presented a bibliography of North American records and Fulmek (1968) listed it as associated with 6 of the 7 European species of *Diplolepis*. *G. stigma* is therefore not host specific for it has been recorded from 3 Nearctic galls (Peck, 1963) and 9 Palearctic galls (Fulmek, 1968). Blair (1945a) found the species attacking *Periclistus brandtii* Er. in the galls of *D. rosae*. Other than these host records, very little is known of its biology.

The same gall collections mentioned previously were used in tabulating the incidence of *G. stigma* eggs and larvae in the *D. polita* galls collected in 1969 (Table 3). Larvae of *G. stigma* were found in 21% of the mature galls collected August 17-23, 1968 and in 12.5% of the mature galls collected August 22, 1969 (Fig. 21). *G. stigma* at George Lake is univoltine, although Niblett (1947) found that a few adults associated with British galls emerged in the fall of the first season. Fig. 20 indicates that the George Lake males emerge before females and this was confirmed by field collections. Females are rapid fliers and unless they are found with their ovipositors inserted deep into a gall, they are exceedingly difficult to capture. From gall emergence studies 139 adults were obtained and the sex ratio was 0.561. *G. stigma* has a lengthy period of emergence as indicated by the 42 oviposition observations in Fig. 19 and the presence of eggs both in galls collected in spring and in sucker shoot galls (Table 3). Niblett (1947) found that July and August was the normal emergence period for British populations associated with *D. rosae* galls. I recorded the first oviposition May 23,

Table 2. Incidence of *Eurytoma longavena* eggs, larvae, and pupae in the galls of *Diplolepis polita*. George Lake, Alberta, 1969.

Date	Sample size	% of galls with eggs (hatched & unhatched)	Mean no. of eggs per gall $\pm$ S.D.*	% of eggs hatched	% of galls with larvae	% of galls with pupae
20-V	4	0	0	0	0	0
25-V	55	3.4	1 $\pm$	0	0	0
28-V	54	33.8	1.1 0.4	0	0	0
6-VI	166	78.3	2.1 1.3	38.7	16.0	0
12-VI	156	87.1	2.7 1.3	48.0	44.8	0
20-VI	176	89.2	3.1 2.0	61.0	52.8	0
27-VI	127	85.8	2.2 1.3	80.4	51.1	0
5-VII	119	90.7	2.4 1.6	92.0	63.8	0
14-VII spring	156	—	—	—	47.5	5.0
14-VII sucker	21	26.6	2.5 1.6	0	0	0
23-VII spring	190	—	—	100**	38.2	0
23-VII sucker	106	81.1	2.1 1.2	44.0	41.5	0
22-VIII	275	—	—	100**	32.1	0

\*means are calculated exclusive of galls without eggs

\*\* estimate

spring = galls initiated in the spring only

sucker = galls initiated on sucker shoots only

1969 although the first eggs were not found until June 6, 1969 (Table 3). Laboratory emergence studies (Fig. 20) indicated that the peak emergence occurs after that of *P. pirata* and *E. longavena*.

*G. stigma* eggs are white to transparent and are banana-shaped with one end slightly thicker than the other. The thicker end also has a small knob at the tip. The long ovipositor of the adult enables it to deposit eggs in large, thicker walled galls unavailable to *E. longavena*. The eggs are laid on the inside surface of the gall cavity or directly on the host larvae. Once the eggs hatch, the shells are almost impossible to detect and therefore Table 3 includes only unhatched eggs. Some of the unhatched eggs may have been missed and this could be one explanation for the sudden increase of galls containing larvae in the August 22, 1969 collection (Table 3). Of the 1969 attacked galls 80% contained a single egg and the remainder contained two eggs. The larvae are cannibalistic and the first hatched consumes other eggs pre-



Table 3. Incidence of *Glyphomerus stigma* eggs and larvae in the galls of *Diplolepis polita*. George Lake, Alberta, 1969.

Date	Sample size	% of galls with eggs (unhatched)	% of galls with larva
20-V	4	0	0
25-V	55	0	0
28-V	54	0	0
6-VI	166	9.0	0
12-VI	156	11.5	0
20-VI	176	22.1	0
27-VI	127	13.0	1.0
5-VII	119	3.8	3.4
14-VII spring	156	0	4.5
14-VII sucker	21	5.0	0
23-VII spring	190	0	5.4
23-VII sucker	106	5.6	0
22-VIII	275	0	12.5

spring = galls initiated in the spring only

sucker = galls initiated on sucker shoots only

sent, with the result that no more than one *G. stigma* larva was ever found per gall. Because this species consumes all inhabitants of the *D. polita* galls in which they occur, it plays an important role in the gall community. *G. stigma* larvae were found preying upon the larvae of *D. polita*, *P. pirata*, *E. longavena*, *T. bedeguaris*, and *Habrocytus sp.*, with *P. pirata* the most important prey. Chamber wall tissue was consumed when the attacked gall contained *P. pirata*, indicating that the species is phytophagous as well as entomophagous. Larvae of *E. longavena* and *Habrocytus sp.* were consumed if they were found inside *P. pirata* chambers. Galls attacked by *G. stigma* larvae have their interiors hollowed and other than being larger (Fig. 6), are similar in appearance to normal galls containing only a *D. polita* larva. The larvae consume most of the inner, more succulent tissues of the gall and as a result the damaged gall has an interior lined with several layers of cell particles.

Blair (1945a) gave a brief description of the *G. stigma* larva. The mature larva is white, tapers towards the anterior end and is clothed with long soft hairs (Fig. 10). The head is cordiform and has two deep, elongated fossae that turn dark brown as the larva matures. Mandibles of the mature larva are slender and curved with a denticle on the inner side some distance before the apex (Fig. 16). Larvae overwinter inside the gall and pupate the following season. The pupal stage of laboratory reared specimens lasted about 20 days.

*Torymus bedeguaris* (Linnaeus)

The genus *Torymus* includes both phytophagous and entomophagous species, the latter mainly attacking gall makers and gall inhabitants. According to Huber (1927), genus *Torymus* in North America is known to include 40 species that attack immature stages of Cynipoidea. Of the 106 Nearctic torymids listed by Peck (1963), 7 are recorded from *Diplolepis* galls. Fulmek (1968) listed 103 European species associated with insect galls and recorded 6 of the 7 European *Diplolepis* as hosts. He recorded one *Diplolepis* species known as the host for 10 *Torymus* species. *T. bedeguaris*, a Holarctic species, was found associated with George Lake *D. polita* galls but it was not a common species in the community. Peck (1963) listed three species of *Diplolepis* known as hosts of *T. bedeguaris* and Fulmek (1968) listed 9 European gall formers as hosts. *T. bedeguaris* has not been previously recorded from *D. polita* galls.

Only 132 *T. bedeguaris* adults were obtained in the two years and the sex ratio for the series was 0.404. Clausen (1940) stated that there is a preponderance of females for all species in which sex ratios are known. In the fall of 1968 39 adults emerged from galls collected that spring and the sex ratio of these specimens was 0.435. No adults emerged in the fall of 1969 from galls collected that season, although 44 were obtained once diapause was broken. Sex ratio of these specimens was 0.388.

All *T. bedeguaris* that emerged in the fall of 1968 did so in late August or early September. Emerging at this time, the adults would find sucker shoot galls available for oviposition. Three *T. bedeguaris* were observed ovipositing in sucker shoot galls in 1968 and one in 1969. Eight other females were collected in the field in July and August of 1969, which indicates that the species is active later in the season than other members of the community (Fig. 19). Only 4 adults emerged from the 300 galls used in the spring emergence study (Fig. 20) and their emergence period was after that of most other species. Varley (1941) stated that temperature influenced the fall emergence of *T. cyanimus* Boh., an ectoparasite of *Urophora jaceana* Hering (Tephritidae). Varley (1937) stated that the larvae of *T. cyanimus* attacked the full grown host larvae in August. He found some adults emerging in the fall, but the majority passed the winter in the larval stage and emerged the following spring. In 1947 he reported that although most *T. cyanimus* adults emerged in May, no eggs or larvae were found until August. As an explanation, he suggested that *T. cyanimus* may have an alternative host or the adults may wait from May until August before the eggs are matured and laid. Moser (1965) reported that *T. vesiculus* Moser, an ectoparasite of *Pachypsylla celtidisvesicula* Riley (Psyllidae, Homoptera), has two generations per year with some of the first and all of the second generation overwintering as mature larvae inside the gall. Although it is strange that some *T. bedeguaris* emerged in the fall of 1968 and none emerged in the fall of 1969, the fact that so few specimens were obtained makes it difficult to discuss population trends with any degree of confidence. *T. bedeguaris* may have two generations per year under certain conditions. Their populations may have been high in the spring of 1968, and ensuing conditions may have allowed many of them to emerge in the fall.

No *T. bedeguaris* eggs were identified in any of the 1968 or 1969 gall collections, although they may have been confused with *G. stigma* eggs. Varley (1947) reported that *T. cyanimus* often laid eggs in groups and although several larvae may be found feeding on the same host, only one larva matured. Only four *T. bedeguaris* larvae were found in the August 22, 1969 collection (Fig. 21) and two of these were reared to adults. Ten other adults were obtained from rearing larvae in gelatin capsules. Eight of these were found as first or second instar larvae attached to paralysed larvae of either *D. polita*, *P. pirata*, *G. stigma*, or *E. longavena*. The occurrence of first and second instar larvae late in August indicated that the species may be capable of overwintering as an immature larva and continuing its development

the following season. Hosts of *T. bedeguaris* are completely consumed leaving only an empty cast skin. *T. bedeguaris* matures on a single host.

The mature larva of *T. bedeguaris* (Fig. 22) is white and clothed with more long hairs than the larva of *G. stigma*. It bears both heavy and long sensory hairs and several rows of long integumentary hairs in a band encircling each segment, giving it a distinctly hairy appearance. The posterior end does not taper abruptly as does the larva of *G. stigma*, nor does it have the sunken fossae. The mandibles (Fig. 17) are narrow and acute without denticles and are difficult to locate in the larval cast skins.

#### *Habrocytus* sp. (indet.)

The Pteromalidae contains some of the most common of the Chalcidoidea and many of the species are known to attack larvae of Hymenoptera. The biology of most species remains unknown and Peck (pers. comm.) stated that the entire genus *Habrocytus* requires revision. Specific characters have yet to be worked out. Peck (1963) listed 31 species of *Habrocytus* and recorded 3 associated with *Diplolepis* galls. Fulmek (1968) recorded 15 European species and listed 4 associated with *Diplolepis* galls. The present study is the first record of a *Habrocytus* species from a gall of *D. polita*.

*Habrocytus* sp. larvae were found attacking only larvae of *P. pirata*, although I suspect they attack *D. polita* larvae along with other inhabitants. *P. pirata* chambers are probably completed and the larvae matured before *Habrocytus* sp. oviposits. Varley (1937) suggested that *H. trypetae* Thoms. was not specific in its choice of hosts and would attack other parasites encountered. Blair (1944) found that *H. bedeguaris* Thoms. attacked full grown larvae and pupae of *Diplolepis* and *Periclistus* and that cannibalism often occurred. Callan (1944) suggested that *Habrocytus periclisti* Callan was restricted to *Periclistus brandti* Ratzb., an inquiline in the galls of *D. rosae*. No eggs of *Habrocytus* sp. were found and the first larvae were observed July 5, 1969 (Table 4) crawling over paralyzed *P. pirata* larvae. Only a single larva was found per host and the number of larvae per gall is dependent upon the number of *P. pirata* larva present (Table 4), the maximum recorded was 11. Superparasitism, as Varley (1947) recorded for *H. trypetae*, was not observed, although if several eggs had been laid per host, the first hatched could easily have consumed other eggs or larvae present. Urbahns (1916) in his study of *H. medicaginis* Gahan also found only a single larva was able to develop per host. They destroy their hosts quickly and only a round, black, pellet remains. This pellet is readily visible in dissected galls (Fig. 4) and was used as the species indicator. Urbahns (1916) stated that the larva of *H. medicaginis* can become fully developed in 6 days after its first meal. *Habrocytus* sp. overwintered in the larval stage inside the gall.

Approximately 300 adults were obtained in this study and the sex ratio was 0.491. Callan (1944) reported examining a series of *H. bedeguaris* reared from galls of *D. rosae*, in which the sex ratio was 0.360 and a series of *H. periclisti* in which the sex ratio was 0.490. *Habrocytus* sp. adults emerged late in the season and were the last species in the *D. polita* gall community to emerge under laboratory conditions (Fig. 20). Forty-two observations of oviposition were made, the earliest was June 22, 1969 and the last was August 20, 1969 (Fig. 19). Only two adults were observed ovipositing in sucker shoot galls. Sucker shoot galls may not be readily attacked by *Habrocytus* sp. because few *P. pirata* larvae are able to form inner chambers.

Table 4. Incidence of *Habrocytus* sp. larvae in the galls of *Diplolepis polita*. George Lake, Alberta, 1969

Date	Sample size	% of galls with larvae	Mean no. of larvae per gall S.D. *
20-V	4	0	0
25-V	55	0	0
28-V	54	0	0
6-VI	166	0	0
12-VI	156	0	0
20-VI	176	0	0
27-VI	127	0	0
5-VII	119	1.0	1.0 ± 0
14-VII spring	156	5.0	1.0 0.3
14-VII sucker	21	0	0
23-VII spring	190	23.0	2.7 2.4
23-VII sucker	106	0	0
22-VIII	275	8.1	3.0 1.9

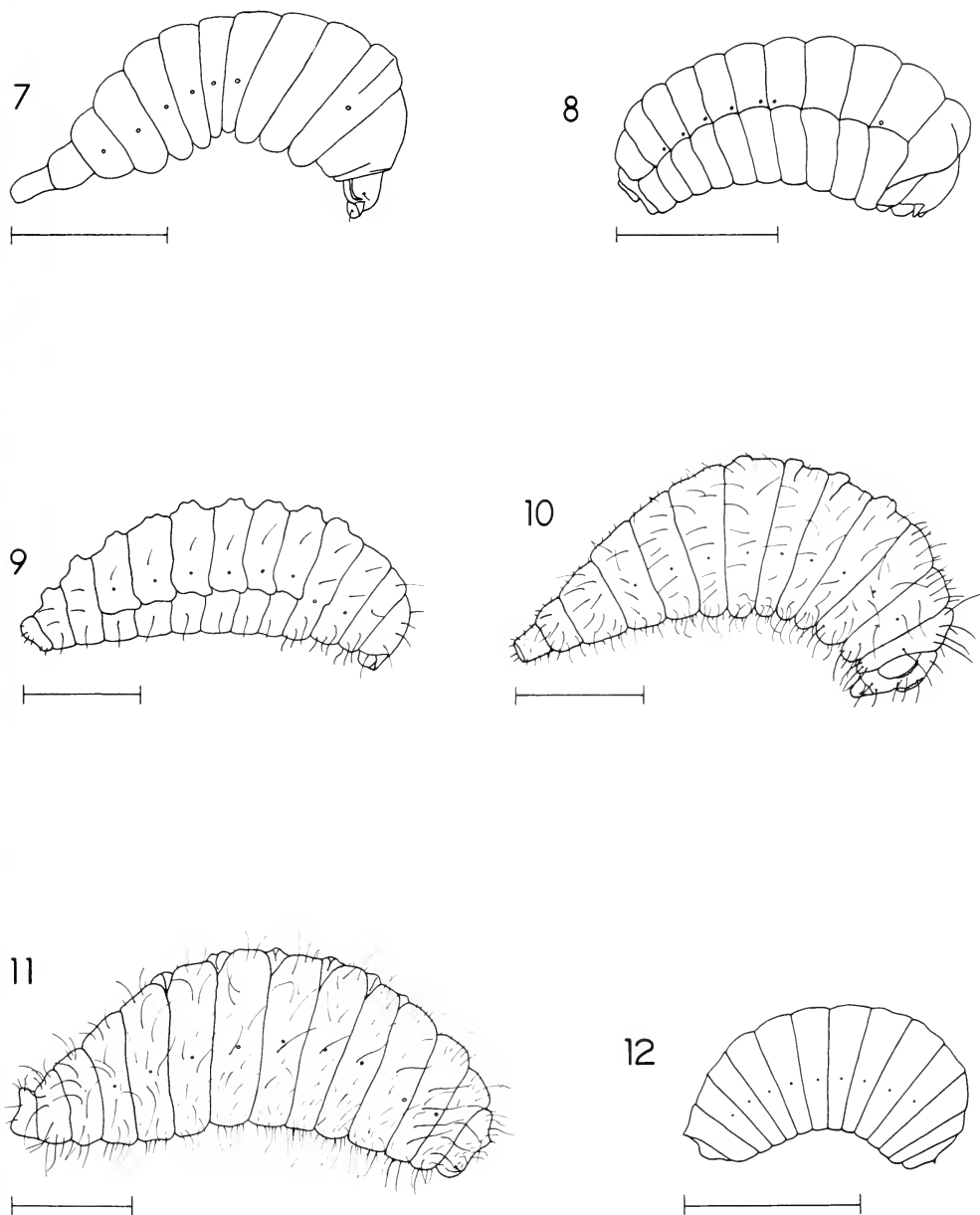
\* means are calculated exclusive of galls without larvae

spring = galls initiated in the spring only

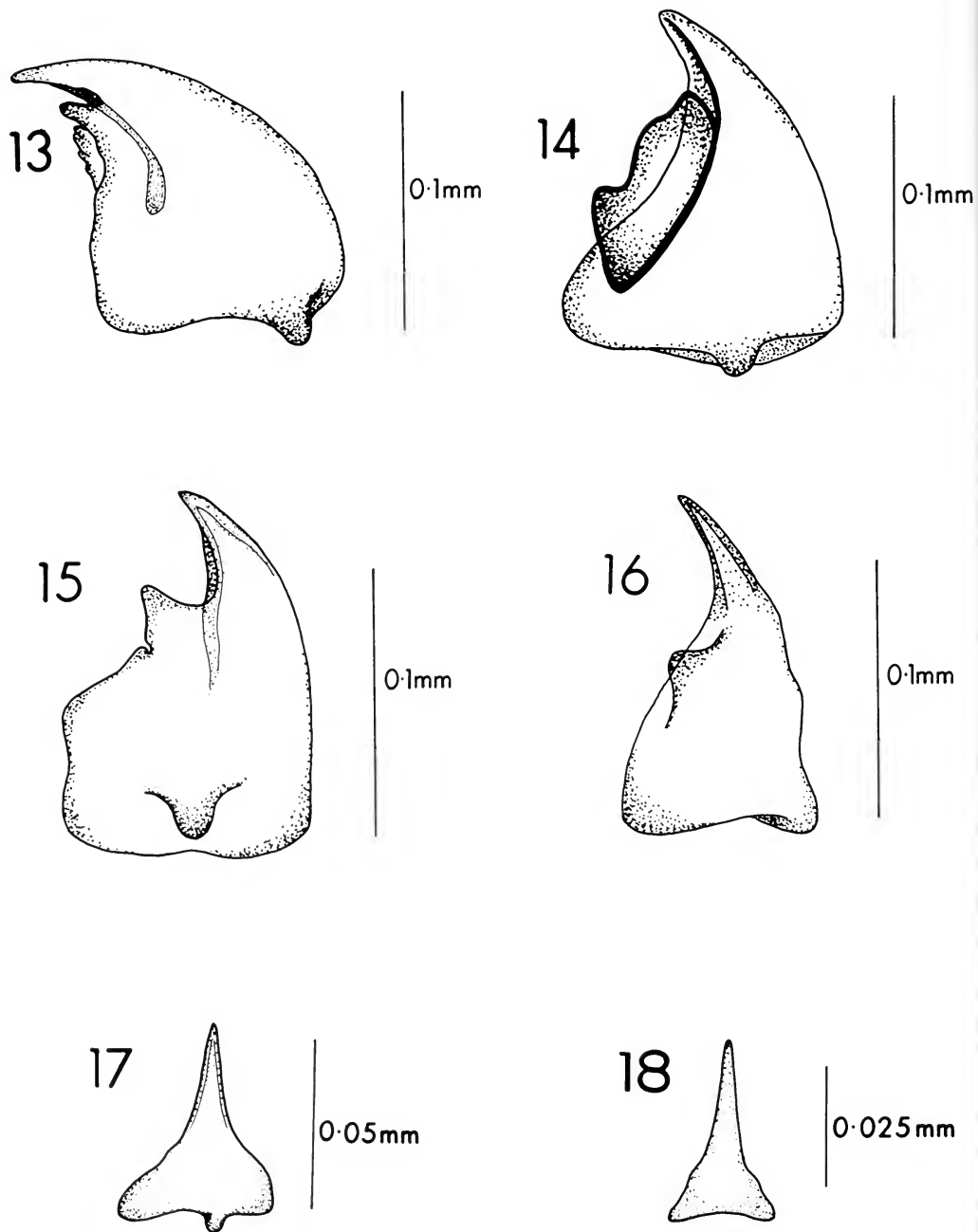
sucker = galls initiated on sucker shoots only

*Habrocytus* sp. is almost entirely univoltine and the adults emerge the following season. Only six fall emergents were obtained in the two years and it is not known whether they oviposited. Niblett (1947) found that a few adults of *H. bedeguaris* emerged in the fall of the first year, but the majority emerged in July and August of the second year. Several mature galls incubated after exposure to 4°C for 3 months were dissected 4 months after inhabitants had stopped emerging. Live *Habrocytus* sp. larvae were found in a few of the *P. pirata* chambers indicating that the species may be capable of an extended larval stage and emergence two seasons later. Many *Habrocytus* sp. larvae are probably consumed by larvae of *E. longavena*, *G. stigma*, and *T. bedeguaris*. The decrease in percentage of galls containing *Habrocytus* sp. larvae on August 22, 1969 (Table 4) is partly due to the feeding of these insects. The inclusion of sucker shoot galls, which contain few if any *Habrocytus* sp. larvae, in the August 22, 1969 collection, also decreased the percentage of galls with larvae.

The mature grub-like *Habrocytus* sp. larva lacks distinguishing features and has weak segmentation (Fig. 12). The integument is smooth and sensory setae are reduced. The tiny mandibles are simple and lack denticles (Fig. 18).



Figs. 7-12. Mature larvae of *Diplolepis polita* gall inhabitants. 7. *Diplolepis polita*. 8. *Periclistus pirata*. 9. *Eurytoma long-avena*. 10. *Glyphomerus stigma*. 11. *Torymus bedeguaris*. 12. *Ilabrocytus* sp. Scale lines all 1.0 mm.



Figs. 13-18. Mandibles of mature larvae found in galls of *Diplolepis polita*. 13. *Diplolepis polita*. 14. *Periclistus pirata*. 15. *Eurytoma longavena*. 16. *Glyphomerus stigma*. 17. *Torymus bedeguaris*. 18. *Habrocytus* sp.

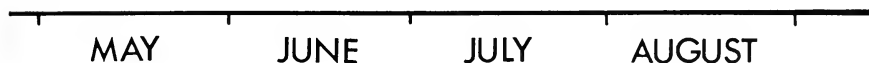
Diplolepis polita (estimated)Periclistus pirataGlyphomerus stigmaEurytoma longavenaHabrocytus sp.Torymus bedeguaris (estimated)

Fig. 19. Oviposition periods recorded for species associated with galls of *Diplolepis polita*, George Lake, Alberta, 1969.

#### SUCCESSION AND CLIMAX IN THE *DIPLOLEPIS POLITA* GALL COMMUNITY: FATE OF MEMBER SPECIES

Mani (1964) briefly introduced the study of plant gall communities. He emphasized that the predator-parasite complex of galls is often considerably larger than that of inquiline and while some galls lack inquilines few, if any, are free from entomophagous inhabitants. The classic paper on this subject is by Varley (1947) in which he discussed factors controlling population density of the knapweed gall-fly. Although there are many factors regulating the gall former population, such as weather and availability of oviposition sites, it is the objective of this section to examine the roles played by each member species in the gall community.

*D. polita* is the central species in the gall community for it causes gall formation and without the gall none of the subsequent species could exist. When the galls first appeared in the spring, *D. polita* predominated. The first three collections in 1969 contained only larvae of *D. polita* (Figs. 21 and 23). The *D. polita* larval population decreased once the eggs of *P. pirata* appeared. By May 28, 1969, only 18.5% of the galls contained a live *D. polita* larva, although only the eggs of *P. pirata* and *E. longavena* were present in the remaining galls (Fig. 21). If *E. longavena* occurred in galls without *P. pirata*, it would undoubtedly devour the *D. polita* larva resulting in a further decrease in the *D. polita* population. The largest population of *P. pirata* larvae was found early in the season (Fig. 23) and because they formed the main food source of the entomophagous species, their dominance soon began to decline. *E. longavena* had the greatest influence on the *P. pirata* population and the number of galls containing the former species had risen substantially by June 20 (Fig. 21). Varley (1947) found that *E. curta* Walker was chiefly responsible for controlling the population density of the knapweed gall-fly. Cannibalistic activities of *E. longavena* probably prevented a major

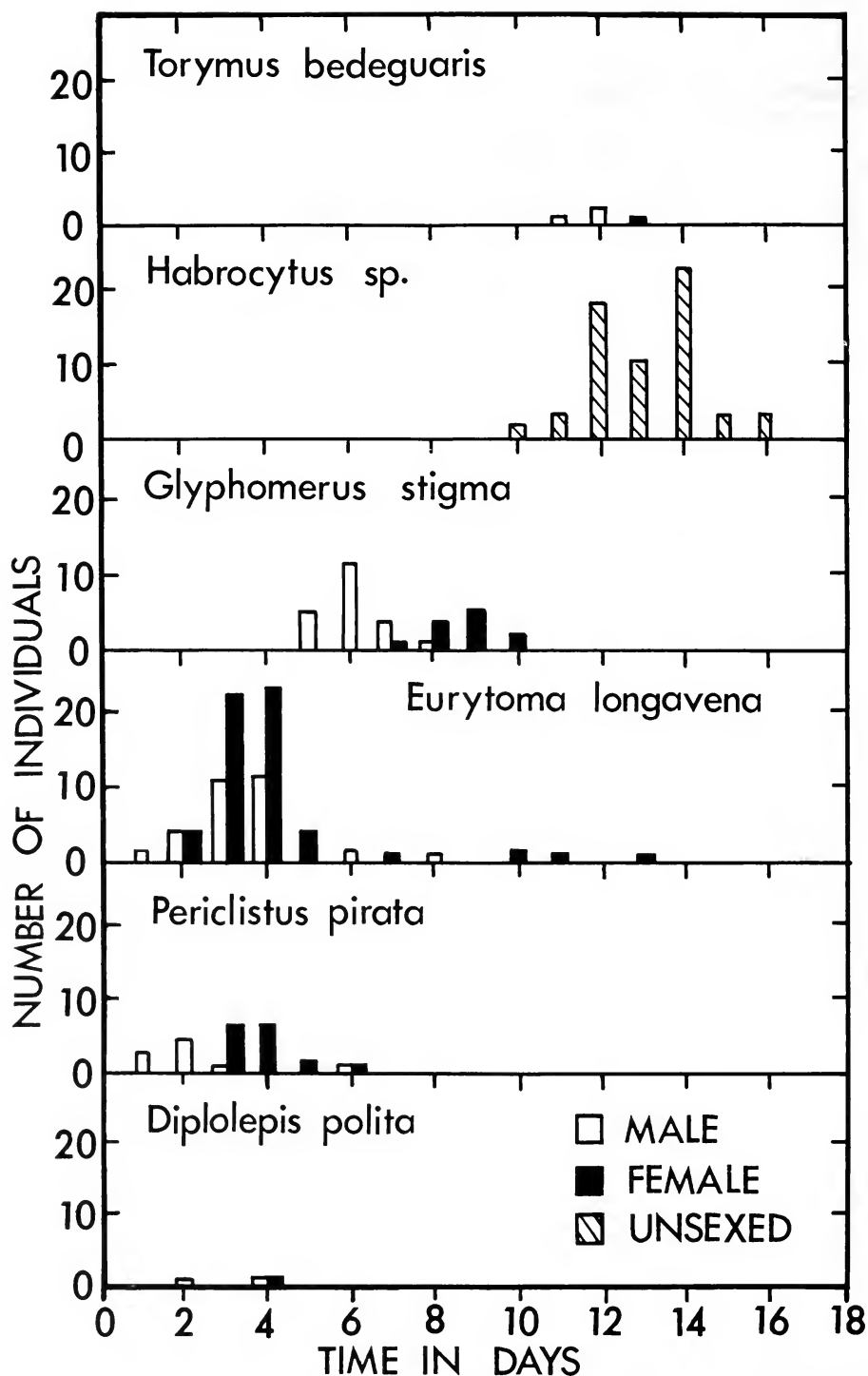


Fig. 20. Spring emergence from 300 galls of *Diplolepis polita* stored at 3°C for 3 months then transferred to 22°. The day of first emergence is day 1. Galls collected at George Lake, Alberta, 1969.



change in the proportion of *E. longavena* to *P. pirata* between June 12 and June 27 (Fig. 23). As the season advanced, feeding activities of *E. longavena* continued to reduce both the *P. pirata* population (Fig. 23) and the number of galls containing *P. pirata* (Fig. 21). Once all *P. pirata* in a gall were consumed, there was an increase in the percentage of galls containing only *E. longavena* (Fig. 21, July 5). *E. longavena* larvae perished if they did not obtain sufficient food before the supply of *P. pirata* was depleted. This was indicated by a decrease in percentage of galls containing *E. longavena* between July 5 and July 14 (Fig. 21). The first larvae of *G. stigma* appeared June 27 although this species was not abundant until later in the season. Larvae of *Habrocytus* sp. had only a slight influence on the *P. pirata* population in the first few collections in which they appeared (Fig. 23).

The occurrence of sucker shoot galls is shown by the reappearance of *P. pirata* and *E. longavena* eggs in the July 14 collection (Fig. 21). *P. pirata* was as detrimental to *D. polita* in sucker shoot galls as in spring initiated galls. The presence of sucker shoot galls did little to increase the *D. polita* population, although it was beneficial to both *P. pirata* and *E. longavena* (Fig. 21). Only 6 galls containing a *D. polita* larva were found in the 107 sucker shoot galls collected July 23. Fall emergence of *E. longavena* enabled this species to oviposit in a large percentage of the sucker shoot galls and as a result the sucker shoot population of *P. pirata* was reduced. Because *G. stigma* larvae consumed all occupants of the galls they inhabited, their presence in 5% of the July 14 galls represented a substantial decrease in the numbers of other larvae. No *G. stigma* larvae were found in sucker shoot galls and therefore the inclusion of sucker shoot galls in the July 23 collection lowers the percentage of galls containing this species (Fig. 21). The presence of *E. longavena* and *P. pirata* in sucker shoot galls increased the relative abundance of these species in the July 23 collection. Had these additional larvae not been present in sucker shoot galls, the proportion of *G. stigma* and *Habrocytus* sp. would have been higher. Most of the *P. pirata* larvae in sucker shoot galls were consumed by mid-August and this also explains the further decrease in the numbers of this species (Fig. 23). Because each *Habrocytus* sp. requires one *P. pirata* larva, their presence helped decrease the number of *P. pirata* in the July 23 and August 22 collections (Figs. 21 and 23).

Fig. 24 shows the inter-relationships of all species composing the *D. polita* gall community. Although *D. polita* was the key species in the community, later in the season *P. pirata* took over the central position of the food web. *P. pirata* had the greatest influence on the *D. polita* population and the presence of this species greatly increased biomass in the community. The remaining entomophagous species depended upon *P. pirata* as their chief source of food. *Habrocytus* sp. larvae were second to those of *E. longavena* as the chief destroyers of *P. pirata*. *G. stigma* and *T. bedeguaris* did not restrict their attack to any one species. Their importance in the community is therefore dependent upon the number of inhabitants in each gall attacked.

The most common cause of empty galls in 1968 and 1969 was food shortage. *E. longavena* and *G. stigma* perished if the galls they inhabited did not contain adequate food for their development. This was less likely for *T. bedeguaris* because they oviposited later in the season when competition between entomophagous species was nearing its climax. The interior of empty galls often contained remains and particles of gall tissue. From the two seasons 8% of the empty galls contained only the remains of first instar larvae of *P. pirata* and had no internal chamber development. Abnormal environmental conditions in the gall cavity or some unusual physiological condition of the plant tissue may have had a toxic effect which killed the gall inhabitants. Sometimes *P. pirata* females may have killed the immature *D. polita* larva and then failed to oviposit. About 15% of the empty galls in the August 22 collection contained fungus. This fungus may have initially attacked plant tissues resulting in the

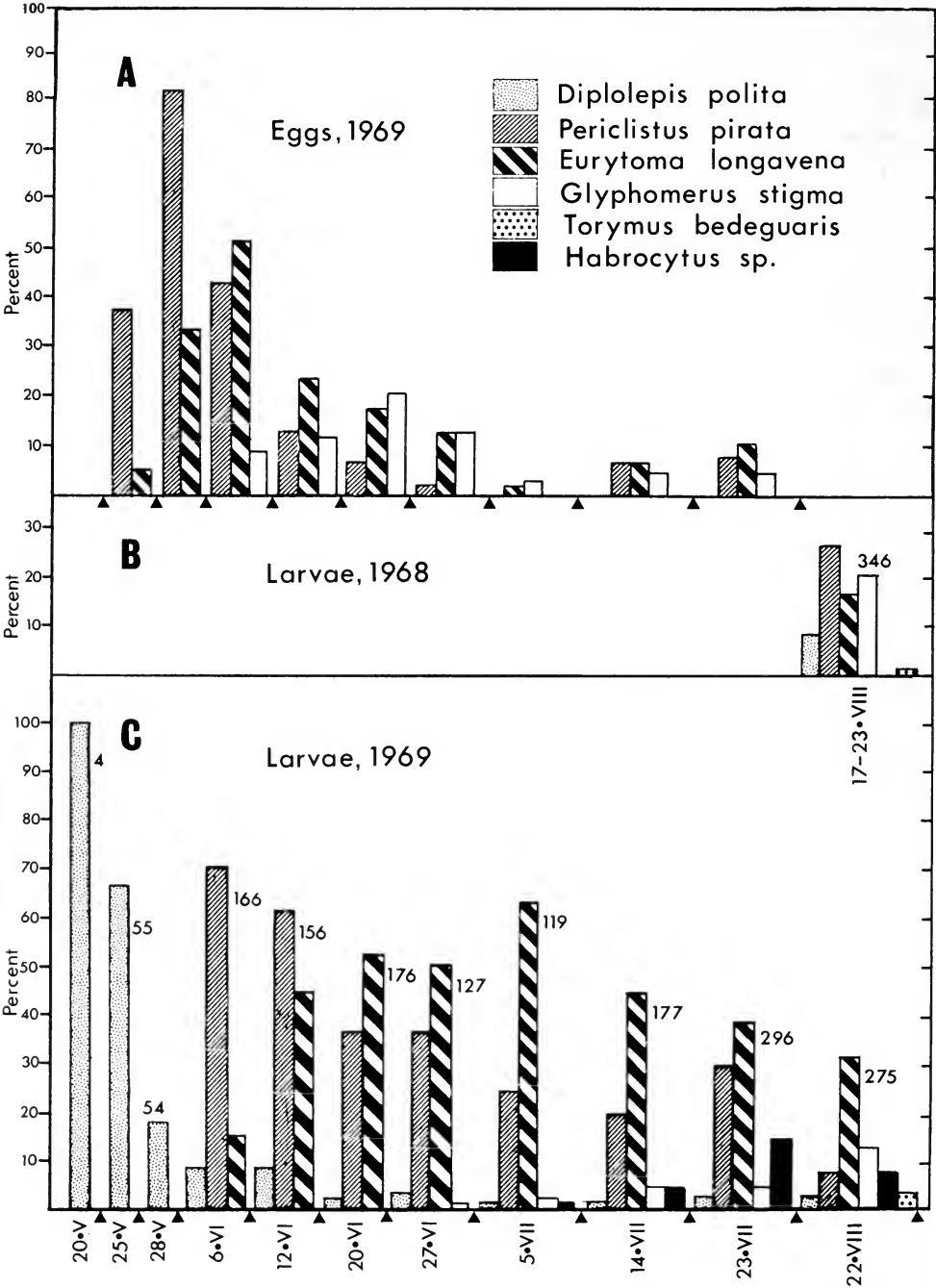


Fig. 21. Percentages of galls containing members of the *Diplolepis polita* gall community. Number of galls in each collection is indicated. George Lake, Alberta, 1968 and 1969. A. Eggs found in galls collected May to August, 1969. B. Larvae found in mature galls collected August 17-23, 1968. C. Larvae found in galls collected May to August, 1969.

death of the inhabitants or it may have developed on dead inhabitants and subsequently spread throughout the gall interior. Disease undoubtedly killed some inhabitants.

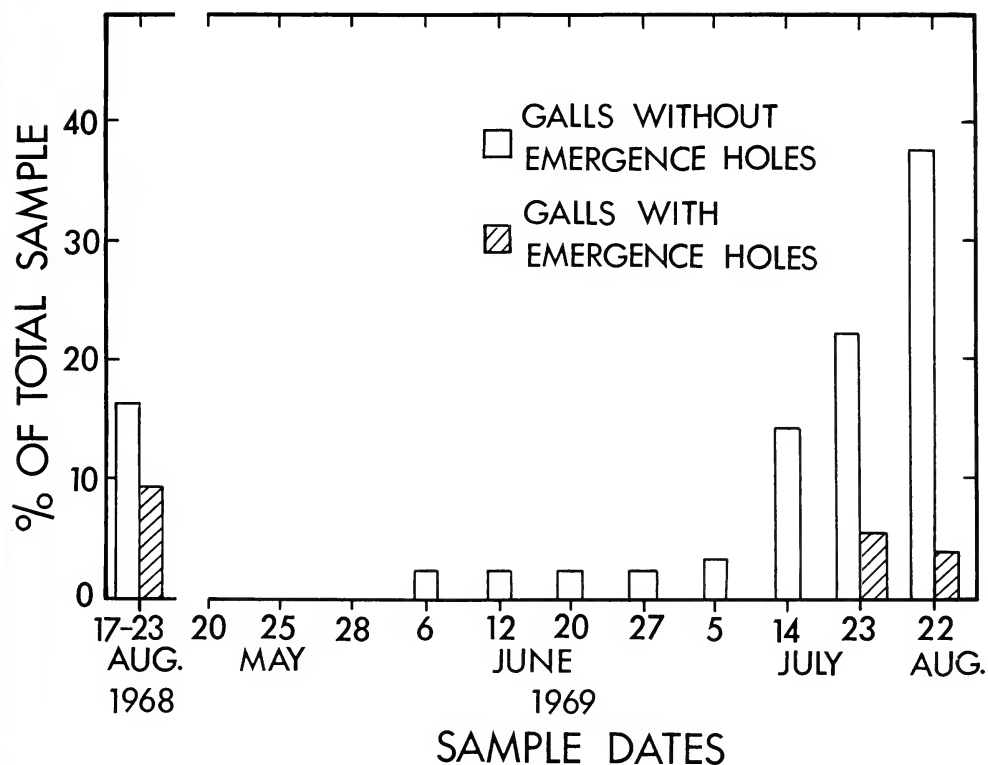


Fig. 22. Incidence of empty *Diplolepis polita* galls, George Lake, Alberta, 1968 and 1969.

Once the galls matured and fell to the ground, no further population additions took place and by analysing collections of these galls, climax of the succession was fixed. Also, after analysing the percentage of galls containing each species (Fig. 21) and the relative abundance of each species (Fig. 23), one can predict population trends for the following season. Predictions of this nature are dependent upon many factors, such as weather, which may have varying effects on the emergence of each species. It was obvious that the occurrence of *D. polita* in 9% of the 1968 mature galls was sufficient to allow for an abundance of galls in 1969. This indicates that the *D. polita* gall community is constructed to tolerate low numbers of the gall former. Several authors have found the same for other galls (Askew, 1961,

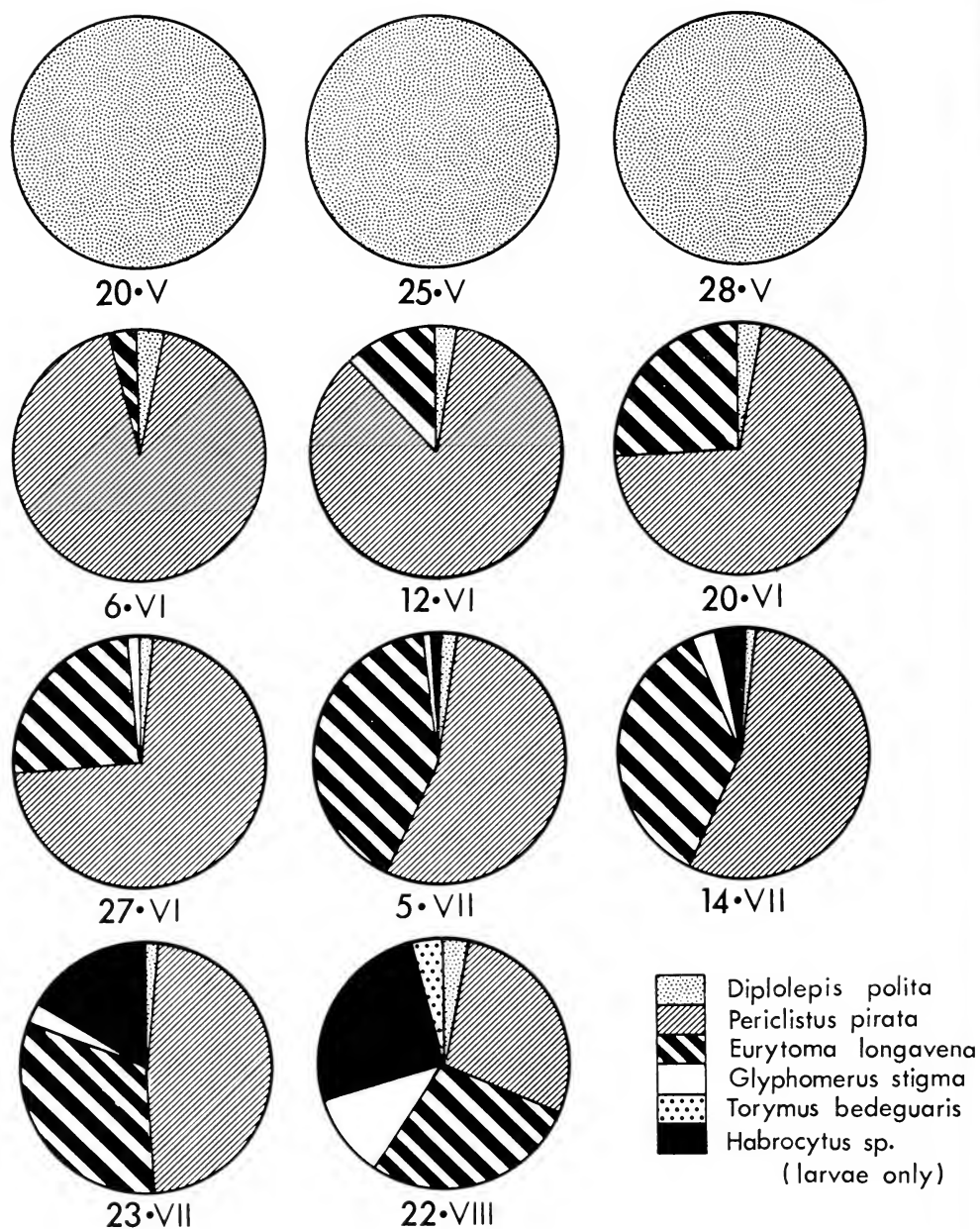


Fig. 23. Incidence of species in the *Diplolepis polita* gall community expressed as percentage of the total populations of gall inhabitants. George Lake, Alberta. 1969.

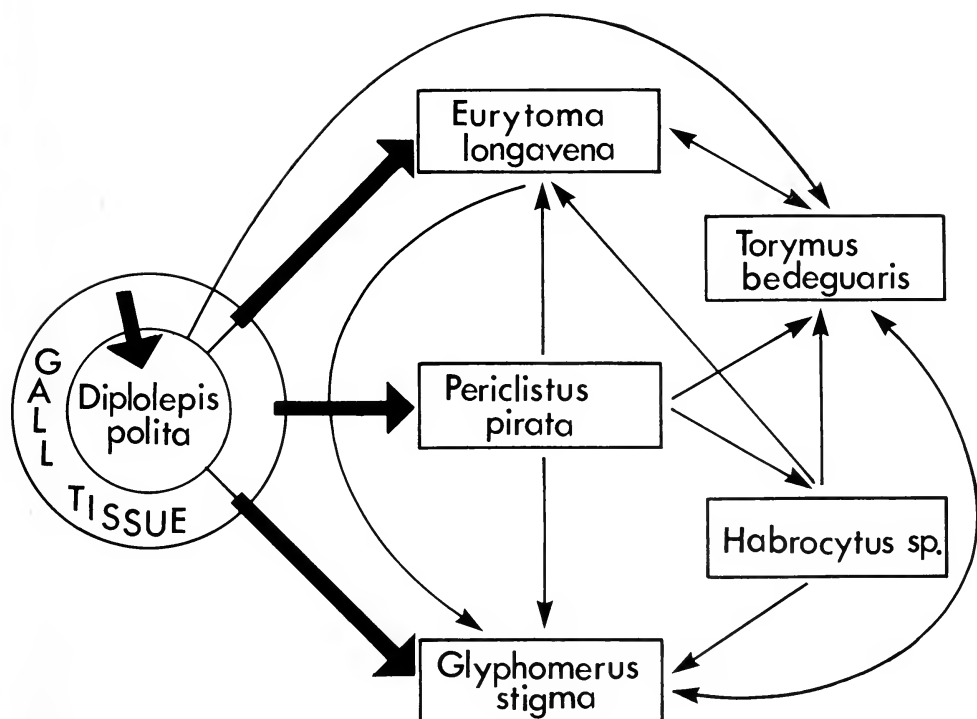


Fig. 24. Food web of species of the *Diplolepis polita* gall community. George Lake, Alberta, 1968 and 1969. Heavy lines represent phytophagous habit, narrow lines represent entomophagous habit.

Evans, 1967; and Gordinier, pers. comm.). By the end of 1969, the *D. polita* population was reduced and initial field observations in 1970 indicated that the galls were less common than in 1969. The occurrence of *P. pirata* larvae in 27% of the 1968 mature galls was chiefly responsible for the decrease in the *D. polita* population by the end of 1969. The availability of *P. pirata* larvae allowed an increase in the *E. longavena* population which in turn was partially responsible for the increase in empty galls. Few *Habrocytus sp.* larvae were found in 1968 mature galls and their abundance in 1969 was probably due to the increase in the *P. pirata* population. The decrease in numbers of *G. stigma* from 1968 to 1969 may be due to some unknown factor affecting only the biology of this species. For the 1970 community structure, I predict a large increase in *D. polita*, because of a decrease in the abundance of *P. pirata*. A decrease in *P. pirata* larvae would also cause a decrease in all entomophagous species and this again would reflect the importance of *P. pirata* in the gall community. This reduction of entomophagous species would allow for a 1971 increase in the *P. pirata* population

which in turn would decrease the *D. polita* population again.

### GROWTH OF *DIPLOLEPIS POLITA* GALLS

The objective of this section is to correlate seasonal changes in gall dimensions with gall contents. In this section the growth rate of galls inhabited by a single *D. polita* larva is compared with the growth rate of galls inhabited by *P. pirata* eggs and larvae.

All studies on gall growth were made in 1969 and the field search for both galls and adults began May 7, 1969. No leaves of *R. acicularis* were out at this date, although those of *Populus* and *Salix* were just appearing. The first *R. acicularis* leaves were found May 8, 1969, in areas of greatest insolation; by May 11, 1969, immature leaves were present on nearly all rose plants. The first *D. polita* galls, 2 leaves with 2 galls on each, were collected May 20, 1969. From May 25, 1969 on, galls were much more common. The diameters of all galls in the 11 random collections described previously were recorded and correlated with gall contents. The mean sizes of galls containing either a *D. polita* larva or *P. pirata* eggs or larvae, for all collection dates, are presented in Tables 5 and 6. In another study, 80 one square metre quadrats were randomly marked off in 4 different rose patches. A total of 134 galls on 30 leaves were found within these quadrats. Each gall was examined and measured approximately every 7 days and data were obtained on their growth rate, shrinkage, senescence, and leaf abscission. Once the galls had fallen, they were returned to the laboratory for dissection. Unfortunately none of these galls contained a larva of *D. polita*.

#### Growth of Galls Inhabited by larvae of *Diplolepis polita* only

The mean diameter of 44 mature galls (Fig. 26) collected in 1968 and containing only a single *D. polita* larva was 3.8 mm (S.D. 0.47). An estimate of the growth curve for normal galls collected in 1969 containing a *D. polita* larva is shown in Fig. 26. By studying growth curves of individual plot galls, it was estimated that the maximum size of normal *D. polita* galls occurred around the middle of July. After this date there was shrinkage and the final size due to gall maturation was reached by the middle of August. The average amount of shrinkage in gall diameter for the 134 plot galls was 0.82 mm (S.D. 0.57) indicating that some of the mature *D. polita* galls collected August 22, 1969 (Table 5) could have been as large as 5.1 mm in diameter. Undoubtedly growth rate and condition of the host plant affects growth rates of attached galls. Factors such as soil condition and availability of light and water affects plant growth rates and must also influence growth rates of galls. Ovipositing in buds not in an optimum condition for galling could affect gall size. Positioning of the gall on the leaflets, the number of leaflets per leaf, and the number of galls per leaflet and leaf, could also influence gall size. Galls growing on older plants may have a different growth rate and final size compared to galls growing on younger plants and sucker shoots.

The first immature sucker shoot galls, all less than 2.9 mm in diameter, were found July 14, 1969. As the season advanced, immature galls on these shoots became more abundant and several collections were made up to August 13. Fig. 25 shows an increase in the number of immature galls less than 4.0 mm in diameter on July 14. Each successive collection contained a decreasing number of immature galls less than 4.0 mm in diameter as maturation processes began (Fig. 25), but the July 14 collection, and the three that followed, showed an increase in the number of immature galls. This increase illustrates the appearance of sucker shoot galls. In the July 23 collection, 106 of the 296 galls were from sucker shoots and 6 of these contained a *D. polita* larva (Table 5). Sucker shoot galls less than 4.0 mm in diameter from two further collections (July 28, 1969 and August 13, 1969) are included in Fig. 25, but their contents are unknown. All galls in the August 22, 1969 collection were

mature and the sucker shoot galls in this collection were combined with spring initiated galls (Fig. 21).

Table 5. Mean diameters of galls containing one larva of *Diplolepis polita*. George Lake, Alberta, 1969.

Date	No. of galls in collection	No. of galls containing <i>D. polita</i>	Mean size of galls containing <i>D. polita</i> larva $\pm$ S.D.	
20-V	4	4	0.8 $\pm$	0.05
25-V	55	35	0.9	0.4
28-V	54	10	1.9	0.6
6-VI	166	15	2.4	1.0
12-VI	156	13	3.2	1.3
20-VI	176	9	3.3	1.2
27-VI	127	4	3.7	1.1
5-VII	119	4	3.4	0.7
14-VII spring	156	2	—	
14-VII sucker	21	-	—	
23-VII spring	190	2	—	
23-VII sucker	106	6	1.7	0.3
22-VIII	275	7	4.3	0.6

spring = galls initiated in the spring only

sucker = galls initiated on sucker shoots only

Immature galls appearing on sucker shoots in July could be due to a delayed hatching mechanism, as mentioned by Yasumatsu and Taketani (1967). They found that *D. japonica* has two periods of gall formation, each appearance of the galls being dependent on the length of time before hatching. They reported that the first group of galls began developing 7 to 10 days after oviposition and the second group began developing 40 days after oviposition. It is possible that the increase in number of immature *D. polita* galls near the middle of July is a result of such a delay. If all *D. polita* eggs were laid around May 1, this second group of immature galls would be developing after approximately 70 days' hatching delay. Although all 13 immature galls collected July 14 contained *P. pirata* eggs, the remains of a *D. polita* larva were found in 5 of them. It appears that hatching of the eggs laid in the buds of sucker shoots is more delayed than in buds of older plants, perhaps because of some physiological condition within the host plant.

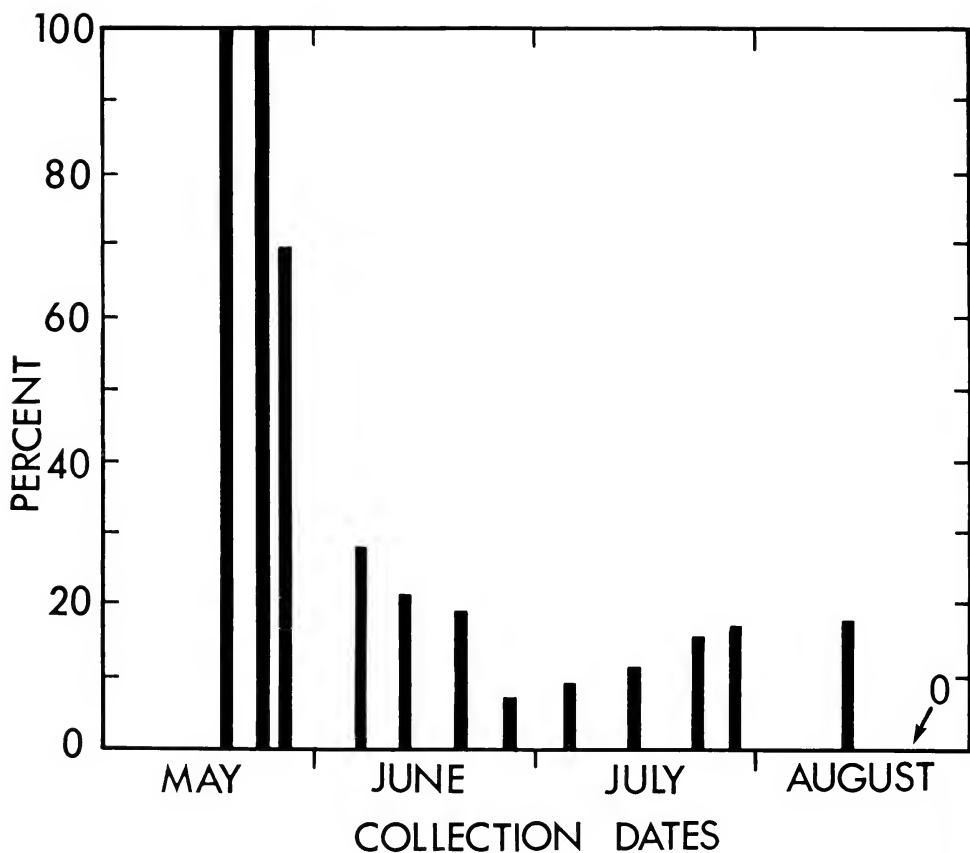


Fig. 25. Seasonal change in the numbers of immature *Diplolepis polita* galls less than 4.0 mm in diameter, expressed as a percentage of each gall collection. George Lake, Alberta, 1969.

#### Growth of Galls Inhabited by *Periclistus pirata*

Although many authors have discussed the position of 'inquilines' in gall communities, few have mentioned their ability to increase gall size. Niblett (1947) was one of the few to show this and stated that the *Diplolepis* gall he was studying showed a great variation in size when inhabited by *Periclistus* larvae. Blair (1945) maintained the opposite for the inquiline *Synergus reinhardi* Mayr in the galls of *Cynips kollari* Hartig, suggesting that inquiline larvae may inhibit gall growth. Evans (1967) stated that if the *Besbicus mirabilis* (Kinsey) gall is inhabited by the inquiline *Ceroptres* species, the immature gall ceases to grow and becomes hard and brittle. Yasumatsu and Taketani (1967) found that galls of *D. japonica* attacked by *Periclistus* sp. were irregular in shape, but they made no mention of size changes.

Eighteen of the 55 *D. polita* galls collected May 25, 1969, contained eggs of *P. pirata* and



in all 18 the larva of *D. polita* had been killed. In the May 28 collection, 44 of 54 galls contained *P. pirata* eggs and their mean size was greater than that of the 10 remaining (Fig. 26). Initiation of inner chamber development by the *P. pirata* larvae was first observed June 20, 1969 and by July 14, chambers were completed in 82% of the galls containing *P. pirata* larvae. The largest spring initiated gall containing *P. pirata* was found July 5, 1969 and was 12.4 mm in diameter.

The increased size of galls containing *P. pirata* eggs (Table 6) results from additional cell proliferation. Substances that cause the proliferation could be injected into gall tissue at the time of oviposition or the eggs may secrete activating substances. Once hatched, larval feeding activities also contribute to the increase in gall size. Even though predators may destroy all gall inhabitants, gall size has usually already been influenced by the *P. pirata* larvae. Predation after *P. pirata* had influenced gall size, results in many large galls without *P. pirata* chambers. Similar findings were also recorded by Niblett (1947).

Table 6. Mean diameters of *Diplolepis polita* galls containing eggs or larvae of *Periclistus pirata*. George Lake, Alberta, 1969

Date	No. of galls in collection	No. of galls containing eggs or larvae	Mean size of galls containing eggs or larvae $\pm$ S.D.	
20-V	4	0	-	-
25-V	55	18 (eggs)	1.6 $\pm$	0.7
28-V	54	44 (eggs)	3.5	0.8
6-VI	166	119 (larvae)	5.0	1.4
12-VI	156	96 (larvae)	6.4	1.5
20-VI	176	64 (larvae)	6.4	1.7
27-VI	127	45 (larvae)	6.5	1.6
5-VII	119	29 (larvae)	7.0	2.0
14-VII spring	156	35 (larvae)	6.9	1.9
14-VII sucker	21	17 (eggs & larvae)	3.2	1.3
23-VII spring	190	33 (larvae)	8.1	1.6
23-VII sucker	106	53 (larvae)	4.6	1.0
22-VIII	275	21 (larvae)	7.2	1.9

spring = galls initiated in the spring only

sucker = galls initiated on sucker shoots only

Galls formed on sucker shoots later in the season are also attacked by *P. pirata*. Another characteristic of sucker shoot galls is that they do not attain the size of *P. pirata* enlarged galls initiated in the spring. The largest sucker shoot gall found was 6.4 mm in diameter. Of the 106 sucker shoot galls found July 23, 1969, 50% contained larvae of *P. pirata*, but 94% of these galls had no inner chamber development. Mean size of these 53 galls was 4.6 mm (S.D. 1.0), significantly smaller than the mean of 8.1 mm (S.D. 1.6) for spring initiated galls (Fig. 26).

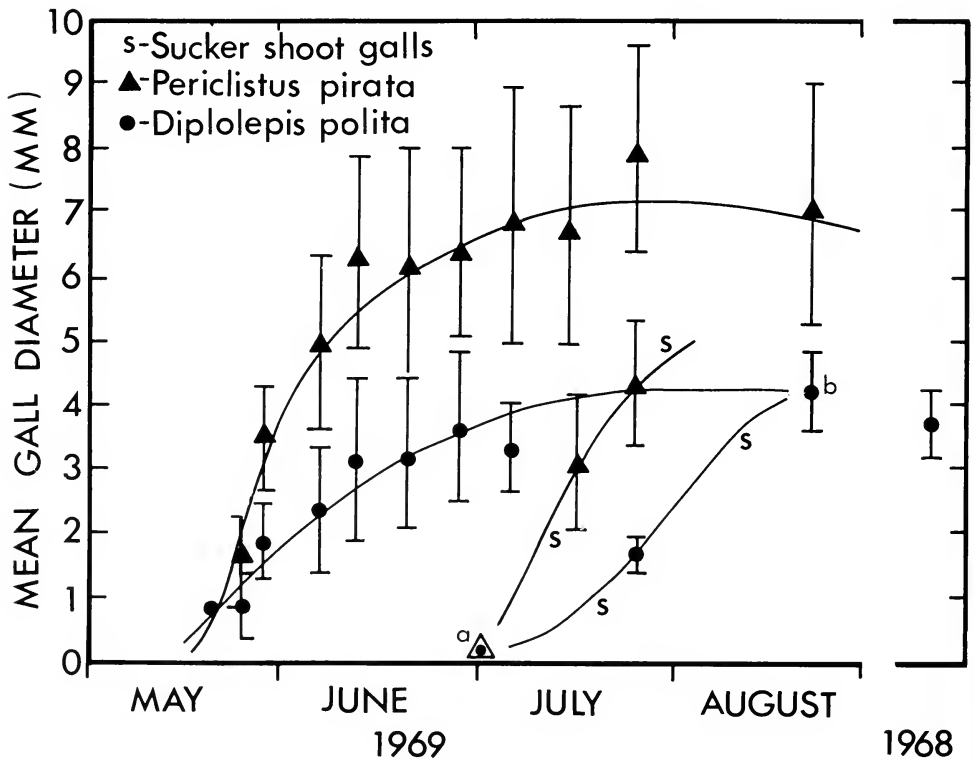


Fig. 26. Seasonal change in the mean size of galls containing a single *Diplolepis polita* larva (solid lines) compared to galls containing *Periclistus pirata* eggs or larvae only (broken lines). Vertical lines indicate one standard deviation each side of the mean. George Lake, Alberta, 1968 and 1969.

#### Gall Senescence and Abscission

Maturation of gall tissue affects nearly all the insects associated with a gall community. Most of the phytophagous larvae are only capable of feeding as long as plant cells remain soft and succulent. All feeding activities of *D. polita* and *P. pirata* larvae are terminated once gall tissues mature. Gall maturation also offers gall inhabitants some protection from predators and parasites. Oviposition activities of predators and parasites are influenced by the degree of tissue maturation. Askew (1961) found that as a gall matured, there was an increase

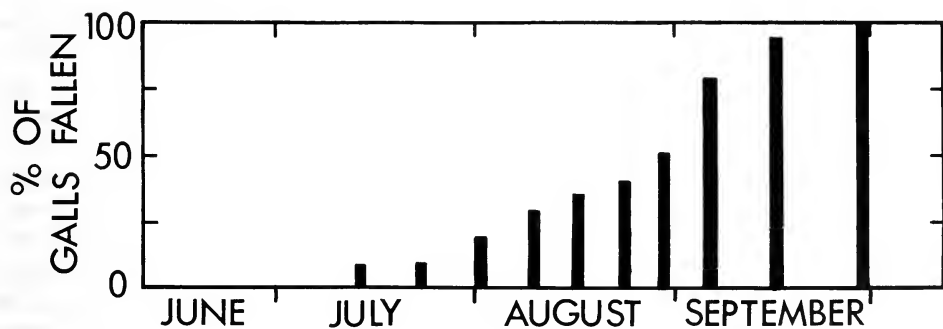
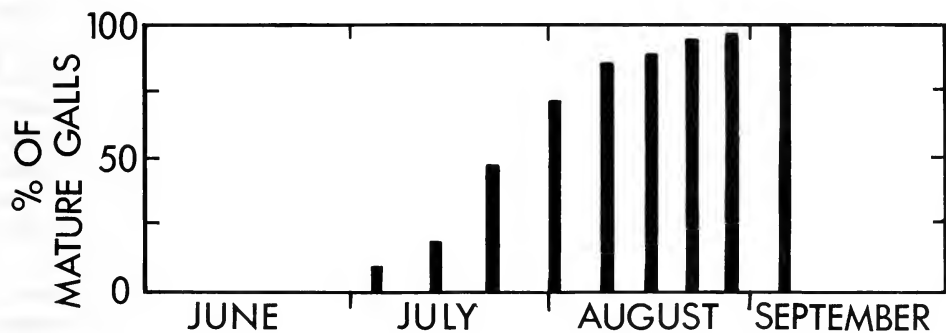
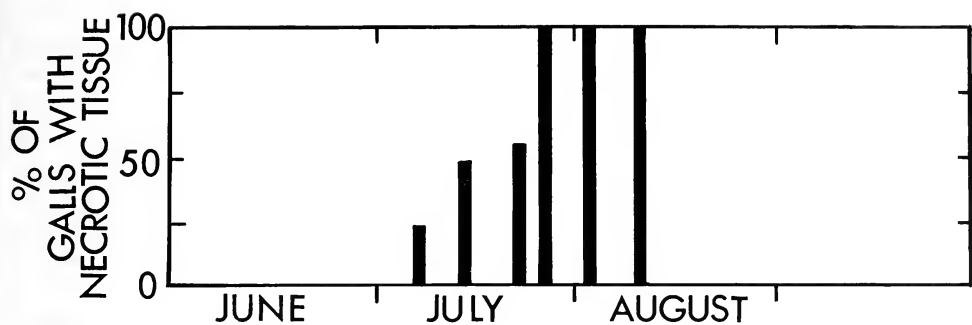


Fig. 27. Percentage of galled leaves with necrotic tissue in collections of spring initiated *Diplolepis polita* galls. George Lake, Alberta. 1969. Fig. 28. Rate of gall maturation of spring initiated *Diplolepis polita* galls found in 80 random plots. George Lake, Alberta. 1969. Fig. 29. Rate of gall abscission of spring initiated *Diplolepis polita* galls in 80 random plots. George Lake, Alberta. 1969.

in the time taken for a parasite to pierce the gall wall. He also measured gall hardness and found that the walls of mature galls of *Cynips divisa* Htg. were 200 times more resistant to crushing than were the walls of immature galls.

Ignoffo and Granovsky (1961) defined gall senescence as the process of turning brown due to tissue necrosis. They considered a gall necrotic when seven-eighths of the surface was brown. Mani (1964) stated that the nutritional deficiency of a leaf beyond the gall is first observed when the gall begins to mature. Early maturation of a galled organ is one of the affects of gall formation on the host and was observed in galled *R. acicularis* leaflets in the present study. The percentage of galled leaves with necrotic tissue, found in the 11 major collections of 1969, is shown in Fig. 27. Only the spring initiated galls are represented in this graph. All galled leaves had necrotic tissues by July 28, 1969, whereas the first discoloration of normal leaves was seen in the last week of August.

*D. polita* galls were considered mature when at least 75% of the gall tissue was dark brown. The rate of gall maturation was determined by examining the 134 galls found in the random plots described previously (Fig. 28). The first mature gall was observed June 28, 1969 and all were mature by September 6, 1969.

Once a mature gall has fallen to the ground, it can be considered immune to attack by most predators and parasites though rodents undoubtedly consume some fallen galls. The rate of gall abscission was also determined by examining the 134 plot galls. The first plot gall had fallen by July 14, 1969 and all had fallen by September 28, 1969 (Fig. 29). Galls growing in large clusters probably fall before galls growing singly because of their combined weight. Large gall clusters often cause the entire leaf to hang vertically (Fig. 2). Galls with their weight increased by *P. pirata* larvae probably fall before galls containing a single *D. polita* larva. Ignoffo and Granovsky (1961) found that the gall of *Mordwilkoja vagabunda* Walsh (Aphididae) prevented the formation of an abscission layer and the gall may remain on the host for 3 years. Yasumatsu and Taketani (1967) found the first galls of *D. japonica* began falling 39 days after initiation. If the average initiation date for the *D. polita* galls can be considered about the middle of May, then the first galls fell approximately 60-70 days after initiation. *D. polita* galls overwinter on the ground and because they fall before normal leaf abscission occurs, their subsequent covering by the autumn complement of leaves helps to protect the gall inhabitants against winter.

## DISCUSSION

This investigation of the *Diplolepis polita* gall and its inhabitants has revealed many basic features of cynipid gall ecology. It is apparent that by studying cynipid galls, one has the opportunity of gaining new information on such basic concepts of biology as community ecology, insect-plant specificity, plant developmental morphology, and the evolution of specialized insect groups.

*D. polita* is the central character in the gall community although as the season advances its dominance in terms of biomass is soon lost to other gall inhabitants. *Periclistus pirata* is mainly responsible for the rapid decline in the *D. polita* population. The entomophagous inhabitants that subsequently invade the galls depend more on the larvae of *P. pirata* as their source of food than they do on *D. polita* larvae. It therefore can be shown that the gall former prepares requisite conditions for the inquiline, which in turn provides requisite conditions for the entomophagous species. By the end of the season, the community consists of much larger proportions of inhabitants other than the gall former and it is the relative proportions of these inhabitants that determines community structure the following season.

The *Diplolepis* species complex has received little attention and the entire genus is in need of taxonomic revision. Several of the names in use are incorrect. Species have been distinguished mainly by their external morphology and because the species exhibit limited variation, use of many of these characters may have led to the taxonomic problems.

A great deal has yet to be learned about the biology of *D. polita* and for that matter, all *Diplolepis* species. Adult *D. polita* can undoubtedly be observed in the field if the researcher is at the right place at the right time. Condition of the host plant at the time of oviposition and gall initiation should be easily delineated. Surprisingly little is known about the induction of cynipid galls. Plant biochemists and morphologists would undoubtedly be interested in learning of the chemical stimuli these insects have evolved to cause cell hypertrophy and hyperplasy. The various stages of gall development from the time of oviposition to gall maturity may reveal structural features that influence activities of the associated insects. The presence of males in the *D. polita* population indicates that normal sexual reproduction occurs and in light of theories of north-south gradations in parthenogenesis, larger populations of all northern species should be examined. The appearance of sucker shoot galls also requires further investigation. If ovipositing females can be handled in the field, controlled ovipositions in both spring and sucker shoot host plants and subsequent observations of gall development should reveal whether there is a delay mechanism in initiation of sucker shoot galls.

From the data obtained on the biology of *Periclistus pirata*, it is apparent that inquiline have an important role in cynipid gall ecology. They take an important position in the community and grossly modify the normal gall structure. Exactly how *Periclistus* disposes of the *Diplolepis* larvae requires further investigation. Because *D. polita* galls were observed to enlarge even before the *Periclistus* eggs hatched, it appears that substances inducing further cell hypertrophy come from either the ovipositing females or the unhatched eggs. *Periclistus* larvae may exhibit cannibalism, but this has yet to be determined. It would be interesting to compare the manners in which *Diplolepis* and *Periclistus* stimulate and modify the plant tissues with which they are in contact. From observations of immature *D. polita* galls it appears that the immature *Diplolepis* larva is surrounded by plant tissues when it hatches and subsequent feeding causes cellular hypertrophy and hyperplasy in all directions from the larva. When *Periclistus* larvae feed, the plant cells are stimulated in such a manner that the tissues grow up and around the individual larva. It will be interesting to determine whether other *Diplolepis* galls are modified by *Periclistus* in a similar manner. If the structure of other galls can be modified as extensively as those of *D. polita*, then many of the gall descriptions and illustrations now in the literature for *Diplolepis* may be inaccurate.

Plant morphologists may benefit from studies of cynipid gall developmental morphology. How these insects gain control of morphogenetic potentialities of host organs remains unknown. Galls cannot be regarded as organs, but they are more than tissue abnormalities for they have constant size and structure. An interesting problem for the morphologist would be to determine whether galls and the tissues composing them can be regarded as 'new' structures, morphologically different from familiar structures. Galls of *Diplolepis* have cells and tissues unlike those normally found in the host plant. We require more information on the mechanisms that induce gall cells to divide without reference to the morphogenetic character of the host organ. It may even be easier for morphologists to study processes of form determination in galls than in normal developmental processes in plants. In galls the inducing agent is not part of the physiological mechanism of the plant, but rather is introduced into the plant.

Insect galls afford numerous opportunities for studying insect-plant host specificity and specificity of the inhabitants. It is now known how certain insects are attracted and restrict-

ed to either one or several closely related hosts, but little, if any, attention has been given to why a species is restricted to one organ of the host plant. Why, for example, is *D. polita* restricted to leaves? Would gall tissue develop if immature larvae were transplanted into meristematic tissues of stems or roots? *D. polita* was found only on *R. acicularis*, although *R. woodsii* often grows alongside. Is *D. polita* restricted to *R. acicularis* or does only this host have tissues susceptible to galling when *D. polita* oviposits? Transplanting larvae of *Diplolepis* species into meristematic tissues of other hosts may yield interesting results.

Many theories on how the habits of several closely related hymenopterans may have evolved can be further studied by examining cynipid galls. For example, have the inquiline that induce cell hypertrophy and hyperplasy lost the ability to cause galls, or are they in the process of developing the ability to initiate their own galls? Transplant experiments may provide clues. Two chalcidoid species, *Eurytoma longavena* and *Glyphomerus stigma* were found to be both entomophagous and phytophagous in their larval stages. It would be interesting to know if these species could complete their development on only one food. Has the phytophagous habit of these species which are normally considered entomophagous, developed because of the reduced biomass in monothalamous galls, or do they exhibit the same habit in other *Diplolepis* galls?

A useful contribution to our knowledge of community structure can hopefully be made by continued studies of population assemblages in insect galls. Insect gall communities are simple communities and their attributes can be determined with relative ease. Granted, my definitions and use of community attributes differ somewhat from the classical usage developed by plant ecologists such as Whittaker (1970). But nearly all aspects of community ecology such as diversity, organization, succession, climax, productivity and biomass, and nutrient cycling can be articulated by examining gall communities. Further research will supply data on these various aspects of gall community ecology and it will be of great interest to compare results and conclusions with those of other community ecologists. Zoogeographical studies of *Diplolepis* communities would be valuable. From distribution maps (Lewis, 1959) it appears that *R. acicularis* spread into North America through Beringia. They probably brought *Diplolepis* species with them and comparisons of communities from Alaska to California should provide information useful to those postulating theories of how natural communities evolved (Whittaker and Woodwell, 1972). Studying series of all known *Diplolepis* species, their galls and communities, should reveal a great deal of information about the evolution of the rose gall complex.

In the past, most workers have taken the descriptive approach to studies of plant galls. It has been my aim to consider galls in terms of ecology rather than simply gall morphology or taxonomy of inhabitants. Before botanists can effectively study developmental processes associated with insect galls, information on the ecology of associated inhabitants is required. Botanical information on galls will be found useful in studies of gall formers and associated species. By combining knowledge from various disciplines of biology, we will be in a better position to understand cynipid galls and the intricacies of these fascinating insect-plant relationships.

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AN ANNOTATED LIST OF THE HYDROADEPHAGA (COLEOPTERA: INSECTA) OF  
MANITOBA AND MINNESOTA  
BY J. B. WALLIS<sup>1</sup>

*This paper is based on a manuscript written by the late J. B. Wallis during the 1920's and 1930's. One hundred and sixty-seven species of beetles belonging to the families Haliplidae, Dytiscidae, and Gyrinidae are recorded from Manitoba and Minnesota. One hundred and forty-one species are recorded from Manitoba and one hundred and six from Minnesota with eighty species common to both areas. Notes on collection records and descriptions of the habitat in which certain species are found are given.*

*Quaestiones entomologicae*  
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Introduction by D. J. Larson<sup>2</sup>

This list of species of Hydroadephaga of Manitoba and Minnesota is a brief condensation of a large manuscript written by the late J. B. Wallis. The original manuscript contains descriptions of all of the following taxa, keys to aid in their identification, and collecting and distribution notes. To a large extent, Wallis' keys and descriptions are summaries of previously published works such as H. C. Fall's revisions of *Coelambus* (= *Hygrotus*) (1919), *Agabus* (1922a), *Gyrinus* (1922b), and *Hydroporus* (1923). Almost all of Wallis' original research on water beetles has been published elsewhere, for example in his papers on *Haliplus* (1933a), *Hydaticus* (1939a), *Graphoderus* (1939b), *Ilybius* (1939c) and in other papers which contain descriptions of new taxa (1924, 1926a, 1926b, 1933a, 1933b, 1933c). Because of this, I consider the most important material in the manuscript to be the extensive list of reliably identified species along with the collecting and distribution records. Fall's papers contain many references to specimens which were sent to him by Wallis. Also Wallis' collection contains specimens identified by Fall. The result of this appears to be very close agreement between Fall and Wallis in their species concepts.

The history of this manuscript has not been fully traced. R. D. Bird (1958; pers. com. 1971) stated that Wallis developed an interest in insects through contact with the Criddle family in Manitoba, with Norman Criddle especially encouraging him to specialize in aquatic Coleoptera. H. B. Leech visited Wallis in 1946 or early 1947. At this time Wallis spoke about his manuscript on the water beetles of Minnesota and Manitoba. Leech (*in litt.*, 1971) states: "he wrote it in the late twenties at the request of the Minnesota people who supplied a large collection to be identified and who were to publish it. Then came the depression and with no likelihood of getting it into print he lost heart." Wallis' interest in this work continued at least to 1933, for citations of the literature to that date have been included. However, papers published by W. J. Brown (1937) and Leech (1938, 1939), although directly relevant to the Manitoba fauna, were not cited by Wallis. The original copy of Wallis' manuscript has been deposited in the Department of Entomology, University of Alberta. Copies of it are located in the California Academy of Sciences (H. B. Leech); Saint Cloud State College, Minnesota (R. Gunderson) and the University of Calgary (D. Larson). Most of Wallis' water beetle collection has been deposited in the Canadian National Collection, Ottawa; however some specimens are housed in the insect collection of the Riveredge Foundation, Calgary, Alberta and in the Strickland Museum, University of Alberta.

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In compiling the following list, I have followed Wallis' manuscript as closely as possible. Wallis' names are used consistently, although changes in status are indicated in parentheses. Also, all editorial comments that I have inserted are placed between square brackets. For each included species, the following information is given: name, Leng catalogue number, list of localities arranged alphabetically, and collecting notes. A few taxonomic notes are also included. For the sake of completeness, addenda have been included of names of water beetle species recorded from Manitoba in the literature since 1937 and therefore not given in Wallis' list.

## FAMILY HALIPLIDAE

Genus *Haliplus* Latreille

*Haliplus* (*s. str.*) *strigatus* Roberts. (2321)

*Localities:* MANITOBA - common west of the Laurentian Highland, and as far north as Le Pas.

*Haliplus* (*s. str.*) *longulus* LeConte. (2322)

*Localities:* MANITOBA - throughout the southern part, moderately abundant. MINNESOTA - St. Anthony's Park, rare.

*Haliplus* (*s. str.*) *immaculicollis* Harris.

*Localities:* MANITOBA - abundant throughout. MINNESOTA - abundant throughout.

*Haliplus* (*s. str.*) *blanchardi* Roberts (2319)

*Localities:* MINNESOTA - Itasca State Park, Ramsey Co., St. Anthony, St. Paul.

*Haliplus* (*Paraliaphlus*) *borealis* LeConte. (2317)

*Localities:* MANITOBA - Selkirk, Winnipeg. MINNESOTA - Pine City, St. Peter, not abundant.

*Haliplus* (*Paraliaphlus*) *triopsis* Say. (2301)

*Localities:* MINNESOTA - Le Sueur Co., Ramsey Co., Red Wing.

*Haliplus* (*Paraliaphlus*) *pantherinus* Aubé.

*Localities:* MINNESOTA - Ramsey Co., St. Paul, St. Peter.

*Haliplus* (*Liaphlus*) *connexus* Matheson. (2300)

*Localities:* MINNESOTA - St. Paul, one specimen only.

*Haliplus* (*Liaphlus*) *apostolicus* Wallis.

*Localities:* MINNESOTA - Bussey's Pond (University of Minnesota Campus), Green Lake, Itasca State Park, St. Paul.

*Haliplus* (*Liaphlus*) *subguttatus* Roberts. (2306)

*Localities:* MANITOBA - generally distributed in southern half. MINNESOTA - Cramer, Hubbard Co., Ramsey Co., St. Paul; abundant.

*Haliplus* (*Liaphlus*) *canadensis* Wallis

*Localities:* MANITOBA - Victoria Beach, Winnipeg, Winnipeg Beach.

*Haliplus* (*Liaphlus*) *cribrarius* LeConte. (2305)

*Localities:* MANITOBA - generally distributed as far north as Mile 256, Hudson's Bay Railway. MINNESOTA - Cook Co., Grand Rapids, Hibbing, Itasca State Park.

Genus *Peltodytes* Regimbart

*Peltodytes* *edentulus* LeConte. (2337)

*Localities:* MANITOBA - generally distributed in southern half; abundant. MINNESOTA - generally distributed; abundant.

*Peltodytes tortulosus* Roberts. (2324)

*Localities:* MANITOBA - Winnipeg Beach (type locality); generally distributed in southern third, though not abundant. MINNESOTA - Ely, Minneapolis, Pelican Rapids, Ramsey Co., St. Paul (Track Pond).

It is interesting to note that this species seems to be extending its range for one can scarcely suppose that it could have been overlooked in such a well hunted place as Toronto, Canada, from which locality I recently received a number of specimens, and in 1931 it was taken at Quebec City.

FAMILY DYTISCIDAE  
SUBFAMILY LACCOPHILINAE

Genus *Laccophilus* Leach

*Laccophilus maculosus* (Germar). (2351)

*Localities:* MANITOBA - moderately common in the southern part of the province; not as yet taken north of about 100 miles from the International Boundary. MINNESOTA - generally distributed and common.

*Collecting notes:* Overwintering is apparently in rivers as specimens were taken by Mr. E. Criddle in the Assiniboine River at Aweme, Manitoba, on January 9, 1928.

*Laccophilus inconspicuus* Fall (2354) (= *biguttatus* Kirby)

*Localities:* MANITOBA - common throughout as far north as Le Pas; probably extends much farther north. MINNESOTA - two records only - a single specimen from Benson (23.viii.22) and one from Ramsey Co. (11.iv.22) - both taken by W. E. Hoffman; doubtless occurs all through the northwestern part of the state.

SUBFAMILY HYDROPORINAE

Genus *Hydrovatus* Motschoulsky

*Hydrovatus pustulatus* Melsheimer.

*Localities:* MINNESOTA - Hennepin, Le Sueur Co., Mora, St. Paul.

Genus *Desmopachria* Babington

*Desmopachria convexa* Aubé (2374)

*Localities:* MANITOBA - Selkirk, Victoria Beach, Winnipeg. MINNESOTA - Hennepin Co., Benson, Ramsey Co., St. Paul.

*Collecting notes:* Occurs in very shallow water among debris and roots.

Genus *Bidessus* Sharp

*Bidessus flavicollis* LeConte. (2385). [placed in genus *Liodessus* Guignot by Young, 1969.]

*Localities:* MINNESOTA - Lake Emily, Lake Jefferson, St. Peter; rare.

*Bidessus affinis* Say. (2390). [Placed in genus *Liodessus* Guignot by Young 1969.]

*Localities:* MANITOBA - common everywhere, as far north as Mile 214, Hudson's Bay Railway. MINNESOTA - Hennepin Co., Le Sueur Co., Minneapolis, St. Paul.

*Collecting notes:* Found in shallow waters with muddy bottoms.

*Bidessus granarius* Aubé. (2398). [Placed in genus *Urarus* Guignot by Young, 1969.]

*Localities:* MINNESOTA - Bussey's Pond, "Minn.", St. Paul.

Genus *Hygrotus* Stephens

*Hygrotus acaroides* LeConte. (2407)

*Localities:* MANITOBA - Winnipeg (type locality of race *winnipeg* Wallis), Rosebank, Thornhill. MINNESOTA - Benson, St. Paul.

*Hygrotus farctus* LeConte. (2405)

*Localities:* MANITOBA - Winnipeg.

*Collecting notes:* The single Winnipeg specimen was found in a little pool in the bed of a partially dried up rivulet in the woods (24.v.1922).

*Hygrotus punctatus* Say (=sayi Balfour-Browne, 1944)

*Localities:* MANITOBA - abundant everywhere. MINNESOTA - abundant everywhere

*Hygrotus turbidus* LeConte. (2408)

*Localities:* MANITOBA - not uncommon southward. MINNESOTA - Booker Co., St. Paul. St. Peter; apparently rare.

*Hygrotus dispar* LeConte. (2409)

*Localities:* MANITOBA - Le Pas, Winnipeg; uncommon. MINNESOTA - Hennepin Co., Owatonna, Rochester; uncommon.

*Hygrotus compar* Fall. (19174)

*Localities:* MANITOBA - Aweme, Winnipeg; rare.

*Hygrotus suturalis* LeConte. (2413)

*Localities:* MANITOBA - Generally distributed, not common in the south, rather plentiful northward. MINNESOTA - Warroad.

*Collecting notes:* Found usually in clear water.

*Hygrotus sellatus* LeConte. (2414)

*Localities:* MANITOBA - in southern third; not common. MINNESOTA - Nicollet Co.

*Collecting notes:* In weedy ponds.

*Hygrotus canadensis* Fall. (19178)

*Localities:* MANITOBA - Winnipeg (type locality); common in southern half of province. MINNESOTA - Hennepin Co., Hibbing, Ramsey Co., St. Anthony's Park; probably all through the northern half of the state.

*Collecting notes:* Prefers clear water.

*Hygrotus patruelis* LeConte. (2412)

*Localities:* MANITOBA - common in southern third, not yet taken in the northern two thirds. MINNESOTA - Grand Rapids, Hennepin, Ottertail Co., St. Anthony's Park.

*Collecting notes:* Prefers clear water.

*Hygrotus nubilus* LeConte. (2420)

*Localities:* MINNESOTA - St. Paul (one specimen).

*Hygrotus punctilineatus* Fall. (19183)

*Localities:* MANITOBA - occasional throughout southern part.

*Collecting notes:* This species is occasionally found in normal(fresh water) situations but the only station where I have taken it commonly is in a small pond only a hundred yards or so from the saline Cobb's Lake near Baldur, Manitoba. I have not had the water of this pond analysed but judging from the vegetation, its chemical contents, while clearly saline or alkaline, differ greatly from the near-by Cobb's Lake.

*Hygrotus tumidiventris* Fall. (19182)

*Localities:* MANITOBA - distributed in waters of a certain type of alkalinity, occasionally taken elsewhere.

*Collecting notes:* Specimens of *tumidiventris* were common in the locality described above under *punctilineatus* but this species is apt to be found in situations where the water is more usual.

*Hygrotus masculinus* Crotch. (2419)

*Localities:* MANITOBA - abundant in Shoal Lake, 35 miles or so northwest of Winnipeg; only accidental elsewhere.

*Collecting notes:* *masculus* adults prefer water containing a high percentage of magnesium salts. The only place in Manitoba where I have taken *masculus* is in Shoal Lake, which appears to be quite rapidly drying up. Much of its bed is now dry, and its water is strongly reminiscent of epsom salts. While covering a number of square miles, it is everywhere very shallow and contains no vegetation except algae, even the edges almost everywhere being without rushes or grass. Naturally, being so shallow and extensive, it is subject to rapid fluctuations of level according to the direction and strength of the wind, often fifteen or twenty minutes making a difference between a dry area and six or eight inches of water. The bottom is slimy mud plentifully sprinkled with stones. Specimens of *masculus* appear to prefer water five or six inches deep and to hide under and around stones.

*Hygrotus salinarius* Wallis. (19188)

*Localities:* MANITOBA - Baldur (Cobb's Lake, type locality), Salt Lake near Strathclair, southern end of Lake Winnipegosis.

*Collecting notes:* *salinarius* adults prefer water strongly impregnated with common salt.

*Hygrotus unguicularis* Crotch. (2421)

*Localities:* MANITOBA - probably throughout the province; rare southward but moderately common at points on the Hudson's Bay Railway, increasingly so northward to Mile 474.

*Hygrotus dentiger* Fall. (20764)

*Localities:* MANITOBA - Thornhill (one specimen).

*Collecting notes:* This species was taken by Mr. F. S. Carr in saline lakes in Alberta, and I took it quite commonly in a pond of moderate salinity or alkalinity near Roche Percee, Saskatchewan. In this pond were specimens of many species found also in fresh water so that its saline content could not have been very great.

*Hygrotus impressopunctatus* Schaller. (2424)

*Localities:* MANITOBA - throughout the province except perhaps in the extreme north; abundant. MINNESOTA - throughout the state, abundant.

Genus *Hydroporus* Clairville

*Hydroporus (Heterosternus) undulatus* Say. (2447)

*Localities:* MANITOBA - Aweme, Husavick, Mile 214 Hudson's Bay Railway, Rosebank, Winnipeg. MINNESOTA - apparently fairly generally distributed. [Note. - Wallis treated *consimilis* LeConte as a valid species. However, he states that "extremes of these two species (*undulatus* and *consimilis*) are easy to separate but I must confess after examining hundreds of specimens from one locality ...that most of these could just as well be called one as the other." Here, the names *consimilis* and *undulatus* are treated as synonyms]

*Hydroporus (Heterosternus) clypealis* Sharp. (2452)

*Localities:* MINNESOTA - one female, Red Wing (30.ix. 1923, W. E. Hoffmann).

*Hydroporus (Heterosternus) vittatus* LeConte. (2465)

*Localities:* MANITOBA - Fork River, Winnipeg (several stations). MINNESOTA - Grand

Marais (one female doubtfully placed here).

*Collecting notes:* Only occasionally and locally being not rare. On one occasion I took several dozen adults in little pools in the bed of a partially dried up creek in East Kildonan just north of Winnipeg.

*Hydroporus (Heterosternus) sericeus* LeConte (2466) (= *superioris* Balfour-Browne).

*Localities:* MANITOBA - generally distributed, except possibly in the extreme north. MINNESOTA - generally distributed.

*Collecting notes:* Locally very abundant in clear but weedy water.

*Hydroporus (Heterosternus) solitarius* Sharp. (2467)

*Localities:* MANITOBA - Mile 214 Hudson's Bay Railway.

*Collecting notes:* Specimens of this species were quite common in July 1917 in deep water in the Piquetenay River, swimming close to the almost perpendicular surface of the rock to which they frequently clung.

*Hydroporus (Heterosternus) pagus* Fall. (19220)

*Localities:* MANITOBA - 16 miles e. Aweme; Township 6, Range 9 East.

*Collecting notes:* Adults inhabit larch or spruce swamps, where the water is cold.

*Hydroporus (Heterosternus) stagnalis* Gemminger and Harold. (2521)

*Localities:* MANITOBA - Stonewall

*Collecting notes:* Taken only in an old quarry test hole in a limestone formation.

*Hydroporus (Heterosternus) planiusculus* Fall. (19224)

*Localities:* MANITOBA - 16 miles e. Aweme. MINNESOTA - Chester, Olmsted Co., St. Peter.

*Collecting notes:* Adults are moderately abundant in the water of a cold rivulet fed by a spring issuing from the sand hills near the banks of the Assiniboine River about 16 miles east of Aweme. There is a peculiar formation here known locally as the "Devil's Punch-bowl", and at the bottom of this is the spring and rivulet mentioned above. Where the rivulet expands and becomes more or less choked with specimens of *Chara*, adults of *planiusculus* may usually be found in some numbers.

*Hydroporus (s. str.) dichrous* Melsheimer. (2510)

*Localities:* MINNESOTA - Le Sueur Co., Rochester, St. Anthony Park, St. Paul, St. Peter. *Hydroporus (s. str.) melsheimeri* Fall. (2511)

[Note. - The description of this species and the list of localities is missing from Wallis' manuscript. The species almost certainly occurs in Manitoba.]

*Hydroporus (s. str.) dentellus* Fall. (2506)

[Note. - This species is treated in Wallis' key to the Minnesota-Manitoba species of *Hydroporus*, and is not in the text of the manuscript, probably because inserted page which also contained the discussion of *H. melsheimeri* was lost. I have seen Manitoba specimens of *dentellus* collected by Wallis (Aweme, Strickland Museum, University of Alberta.)

*Hydroporus (s. str.) notabilis* LeConte. (2518)

*Localities:* MANITOBA - fairly generally distributed throughout, at least as far north as Mile 332 Hudson's Bay Railway. MINNESOTA - Mendota

*Hydroporus (s. str.) arcticus* Thomson. (2519)

*Localities:* MANITOBA - Churchill ( 2 specimens, 5 & 11.ix. 30, F. Neave). Fall (1923) pointed out that this species may well prove to be but a race of *notabilis* LeConte.

*Hydroporus (s. str.) niger* Say. (2514)

*Localities:* MINNESOTA - Le Sueur Co., St. Paul, St. Peter.

*Hydroporus (s. str.) columbianus* Fall. (19215)

*Localities:* MANITOBA - not common, but widely distributed in the south.



*Hydroporus (s. str.) rectus* Fall. (19209)

*Localities:* MANITOBA - Aweme, Mile 256 Hudson's Bay Railway, Township 7 Range 11E.

*Hydroporus (s. str.) despectus* Sharp. (2495)

*Localities:* MANITOBA - Aweme, Winnipeg. MINNESOTA - one female from Itasca Park appears to belong here.

*Hydroporus (s. str.) tenebrosus* LeConte. (2493)

*Localities:* MANITOBA - generally distributed well to the north, abundant. MINNESOTA - Le Sueur Co. (1 specimen).

*Hydroporus (s. str.) pervicinus* Fall. (19207)

*Localities:* MANITOBA - Aweme, Onah, Township 7 Range 11E, Transcona. MINNESOTA - Bengall, Hibbing, St. Paul.

*Hydroporus (s. str.) tartaricus* LeConte. (2491)

*Localities:* MANITOBA - Aweme, Hudson's Bay Territory, Winnipeg.

*Hydroporus (s. str.) signatus* Mannerheim. (2508)

*Localities:* MANITOBA - Mile 332 Hudson's Bay Railway. MINNESOTA - Hibbing, Ramsey Co., St. Anthony Park, St. Paul.

*Hydroporus (s. str.) obscurus* Stürm. (2492)

*Localities:* MANITOBA - Mile 214 and Mile 332 Hudson's Bay Railway, Township 7 Range 11E.

*Hydroporus (s.str.) badiellus* Fall. (19206)

*Localities:* MANITOBA - Mile 214 and Mile 332 Hudson's Bay Railway, Township 7 Range 11E.

[Note. - Wallis states that *obscurus* and *badiellus* at least as far as the species are understood here, are very similar and appear to always occur together. Perhaps, at least in Manitoba, these should be treated as only one species.]

*Hydroporus (s. str.) appalachius* Sherman. (2498)

*Localities:* MANITOBA - Aweme, Mile 332 Hudson's Bay Railway, Thornhill, Winnipeg. MINNESOTA - Hennepin Co.

*Collecting notes:* This species is sometimes not uncommon in shallow pools in woodland streams.

[Note. - Wallis lists *occidentalis* Sharp as occurring in Manitoba and Minnesota. This species appears to be western in distribution and probably does not occur in this area. The records for *occidentalis* probably refer to dark specimens of *appalachius*.]

*Hydroporus (s. str.) melanocephalus* Gyllenhal. (19205)

*Localities:* MANITOBA - Churchill, Mile 256 and 332 Hudson's Bay Railway, Township 7 Range 11E.

*Collecting notes:* A species occurring in the colder waters, commoner northward, quite rare southward where it has been taken only in the cold sphagnum moss bogs east of Winnipeg.

*Hydroporus (s. str.) fuscipennis* Kies. (2509)

*Localities:* MANITOBA - universally distributed so far as known; our commonest species. MINNESOTA - St. Anthony's Park.

*Hydroporus (s. str.) striola* Gyllenhal.

*Localities:* MANITOBA - generally distributed and abundant. MINNESOTA - Hennepin Co., Hubbard Co., Mora Co.

*Hydroporus (s. str.) glabriusculus* Aubé. (2500)

*Localities:* MANITOBA - Aweme, Mile 256 and 332 Hudson's Bay Railway, Winnipeg.

*Hydroporus (s. str.) rufinasus* Mannerheim. (2504)

*Localities:* MANITOBA - Mile 332 Hudson's Bay Railway, Township 7 Range 11E., Victoria Beach, Winnipeg.

*Hydroporus (s. str.) tristis* Paykull. (2501)

*Localities:* MANITOBA - quite generally distributed.

*Hydroporus (Deronectes) striatellus* LeConte. (2431)

*Localities:* MANITOBA - second Cranberry Lake (near Cranberry Portage, Hudson's Bay Railway) - two specimens (27.viii. 1930), F. Neave.

*Collecting notes:* Second Cranberry Lake is of a different formation from most of our northern lakes, being in limestone, whereas most of the others are in granite.

*Hydroporus (Deronectes) griseostriatus* DeGeer. (2430)

[Note. - In the manuscript, this species is included in the key to Minnesota-Manitoba species of *Hydroporus*, however the text page dealing with it is missing. The species is no doubt widely distributed in the area.]

*Hydroporus (Deronectes) rotundatus* LeConte [= *elegans* Panzer].

*Localities:* MANITOBA - moderately common throughout. MINNESOTA - Brandon.

*Collecting notes:* in clear weedy streams.

*Hydroporus (Oreodytes) duodecimlineatus* LeConte (probably a synonym of *laevis* Kirby.) (2482)

*Localities:* Mile 474 Hudson's Bay Railway.

*Hydroporus (Oreodytes) scitulus* LeConte.

*Localities:* MANITOBA - Mile 332 Hudson's Bay Railway.

Genus *Laccornis* des Gôzis

*Laccornis conoideus* LeConte. (2532)

*Localities:* MANITOBA - generally distributed in the southern part of the province. MINNESOTA - Owatonna (one specimen).

*Collecting notes:* It is not uncommon in spring in ditches and in temporary ponds. Later it is found in places where the water keeps fairly cold.

## SUBFAMILY COLYMBETINAE

### Genus *Agabus* Leach

*Agabus seriatus* Say. (2539)

*Localities:* MANITOBA - Aweme, Mile 474 Hudson's Bay Railway, Thornhill. MINNESOTA - Hennepin Co., Le Sueur Co., St. Anthony's Park, St. Paul, St. Peter.

*Collecting notes:* Specimens are found chiefly in waters flowing from cold springs, though the species does not seem to be a denizen of the cold larch swamps.

*Agabus triton* Fall. (19232)

*Localities:* MANITOBA - Winnipeg.

*Collecting notes:* This species is not uncommon in ditches and ponds near Winnipeg in early spring.

*Agabus punctulatus* Aubé. (2551)

*Localities:* MANITOBA - everywhere, even being recorded from Nelson River. MINNESOTA - "Minnesota", Ottertail Co., St. Anthony's Park.

[Note.- The specimens recorded from Nelson River Manitoba could represent *colymbus* Leech 1938: I have not examined them.]

*Agabus semipunctatus* Kirby. (2553)

*Localities:* MANITOBA - rather generally distributed as far north as Mile 24 [ typing error; should perhaps read mile 214, a frequently mentioned locality]. Hudson's Bay Railway. MINNESOTA - "Minnesota", Ramsey Co.

*Agabus sharpi* Fall (19234) (= *falli* Guignot)

*Localities:* MANITOBA - Winnipeg and vicinity.

*Agabus disintegratus* Crotch. (2557)

*Localities:* MINNESOTA - Rochester.

*Agabus ambiguus* Say.

*Localities:* MANITOBA - widely distributed in southern half and quite abundant. MINNESOTA - Le Sueur Co.

*Collecting notes:* This species remains active throughout the winter, specimens having been taken through a hole cut in the ice of the Assiniboine River near Aweme on January 9th, 1928, by Mr. E. Criddle.

*Agabus congener* Paykull. (2560)

*Localities:* MANITOBA - Churchill, Winnipeg.

*Agabus discolor* Harris. (2564)

*Localities:* MANITOBA - Aweme, Mile 332 Hudson's Bay Railway, Onah, Winnipeg; rather abundant. MINNESOTA - Duluth.

*Agabus inscriptus* Crotch. (2559)

*Localities:* MANITOBA - Bird's Hill, Mile 332 Hudson's Bay Railway, Riding Mountain. MINNESOTA - Lake Superior, White Fish Point.

*Agabus canadensis* Fall. (19237)

*Localities:* MANITOBA - abundant in southern half.

*Collecting notes:* In savannah and prairie associations.

*Agabus subfuscatus* Sharp.

*Localities:* MANITOBA - Aweme, Winnipeg. MINNESOTA - Ottertail Co. One female should probably be referred here.

*Agabus phaeopterus* Kirby. (2566)

*Localities:* MANITOBA - quite generally distributed at least as far north as Mile 332, Hudson's Bay Railway. MINNESOTA - Duluth.

*Agabus bicolor* Kirby (2567)

*Localities:* MANITOBA - Aweme, Mile 214 Hudson's Bay Railway Township 1 Range 14E., Township 7 Range 11E.

*Agabus confinis* Gyllenhal. (2563)

*Localities:* MANITOBA - Bird's Hill, Hudson's Bay, Mile 214 Hudson's Bay Railway, Riding Mts., Thornhill, Township 7 Range 11E., Township 14 Range 10E. MINNESOTA-Duluth.

*Collecting notes:* quite rare but widely distributed in cold water, usually in larch swamps.

*Agabus infuscatus* Aubé. (2571)

*Localities:* MANITOBA - Churchill, Mile 332 Hudson's Bay Railway.

*Collecting notes:* Just west of the railway bridge at Kettle Rapids in mid July an outcropping of rock was exposed in the bed of the Nelson River owing to the lowering of the water. On the surface of this rock were several small puddles two or three feet wide and a foot or so deep. Considerable amounts of slimy algae were floating on the surface of the water in these pot holes, and formed several inches of sediment at the bottom. From three or four of these unlikely looking puddles several dozen specimens of *infuscatus* were taken. Specimens were not found elsewhere.

*Agabus arcticus* Paykull. (2576)

*Localities:* MANITOBA - Mile 214 Hudson's Bay Railway and northward to Churchill.

*Collecting notes:* Specimens of this species were common in shallow grassy water in an expansion of the Piquitenay River at Mile 214 Hudson's Bay Railway.

*Agabus ontarionis* Fall. (19238)

*Localities:* MANITOBA - Aweme, Charleswood, Makinak.

*Agabus ajax* Fall. (19239)

*Localities:* MANITOBA - 16 miles east Aweme, Fort Churchill.

*Agabus anthracinus* Mannerheim. (2575)

*Localities:* MANITOBA - generally distributed probably into the far north, quite common.

*Agabus nigroaeneus* Erichson (2579) (= *erichsonii* Gemminger and Harold).

*Localities:* MANITOBA - generally distributed; quite abundant. MINNESOTA - state locality only.

*Agabus pseudoconfertus* Wallis. (20782)

*Localities:* MANITOBA - Bird's Hill, Mile 17 Hudson's Bay Railway, Township 7 Range 11E., Winnipeg.

*Collecting notes:* This species is an inhabitant of the true sphagnum bogs, being found in the small holes in the swamps where a little clear water shows. It is an early spring species and I have taken specimens by breaking an inch or so of ice from the surface and then dredging among the moss which is itself largely imbedded in ice.

*Agabus kenaiensis* Fall. (20778)

*Localities:* MANITOBA - Bird's Hill, Onah, Township 7 Range 11E.

*Collecting notes:* Like *pseudoconfertus*, this species is also an inhabitant of sphagnum bogs.

*Agabus minnesotensis* Wallis.

*Localities:* MINNESOTA - Hennepin Co., (single type).

[Note. - Perhaps the type specimen was erroneously labeled as the species has since been found in the west only (Anderson. 1962).]

*Agabus verus* Brown [= *clavicornis* Sharp (J. Balfour-Browne, 1947)] (21729)

*Localities:* MANITOBA - Churchill.

*Agabus clavatus* LeConte (2577) (= *antennatus* Leech)

*Localities:* MANITOBA - Mile 214 Hudson's Bay Railway, Stonewall, Thornhill, Winnipeg. MINNESOTA - Le Sueur Co., Ramsey Co., St. Paul, St. Peter.

*Collecting notes:* Adults are somewhat local and not usually at all common but I took many specimens in company with *arcticus* specimens in shallow water among grass in a widening of the river at mile 214 Hudson's Bay Railway.

*Apator* (= *Agabus*) *bifarius* Kirby. (2587)

*Localities:* MANITOBA - common throughout the province. MINNESOTA - Owatonna, Ramsey Co., St. Anthony's Park, St. Paul.

Genus *Ilybius* Erichson

*Ilybius pleuriticus* LeConte. (2590)

*Localities:* MANITOBA - generally distributed in southern half but rather uncommon; more abundant at Mile 214 Hudson's Bay Railway. MINNESOTA - Beaver Dam near Ely.

*Ilybius angustior* Gyllenhal. (2595)

*Localities:* MANITOBA - generally distributed and moderately abundant as far north as the limit of trees. MINNESOTA - Olivia.

*Ilybius subaeneus* Erichson. (2589)

*Localities:* MANITOBA - throughout the province at least as far north as within 90 miles of Hudson's Bay. More abundant northward. MINNESOTA - Duluth, Grand Marais, "Minnesota".

*Ilybius biguttulus* Germar (2598)

*Localities:* MINNESOTA - Hibbing, Le Sueur, Two Harbors.

*Ilybius fraterculus* LeConte.

*Localities:* MANITOBA - abundant in southern half. MINNESOTA - throughout the northern half of the state at least.

*Ilybius discedens* Sharp. (2597)

*Localities:* MANITOBA - on the Canadian Shield to Hudson's Bay.

*Collecting notes* - In cold sphagnum bogs.

Genus *Coptotomus* Say

*Coptotomus interrogatus* Fabricius. (2610)

*Localities:* MANITOBA - everywhere as far north at least as Le Pas; very abundant. MINNESOTA - apparently widely distributed and abundant.

Genus *Scutopterus* Crotch (= *Neoscutopterus* F. Balfour-Browne)

*Neoscutopterus angustus* LeConte. (2612)

*Localities:* MANITOBA - Thornhill, Township 7 Range 11E., Winnipeg

*Collecting notes:* Usually found in small mossy pools in larch swamps.

*Neoscutopterus horni* Crotch. (2613)

*Localities:* Aweme, Riding Mts., Township 7 Range 11E.

*Collecting notes:* Found in the same type of habitat as the preceding species.

Genus *Rhantus* Boisduval and Lacordaire

*Rhantus sinuatus* LeConte. (2620)

*Localities:* MINNESOTA - Le Sueur Co., St. Paul.

*Rhantus plebeius* Sharp (= *binotatus* Harris). (2616)

*Localities:* MANITOBA - generally distributed in southern half. MINNESOTA - Hibbing, Grand Marais.

*Rhantus notatus* Fabricius. (2622)

*Localities:* MANITOBA - abundant throughout the southern portion; may be found well towards Hudson's Bay. MINNESOTA - Le Sueur Co., St. Anthony Park; probably generally distributed.

*Rhantus suturellus* Harris [= *wallisi* Hatch cf. Hatch 1953]

*Localities:* MANITOBA - un iversally distributed at least as far north as Mile 214 Hudson's Bay Railway. MINNESOTA - Beaver Dam, Hennepin Co., Lake Co., Olivia, Ramsey Co., St. Peter.

*Rhantus zimmermanni* Wallis (= *suturellus* Harris cf. Hatch 1953)

[Locality list missing from manuscript.]

*Rhantus tostus* LeConte. (2624)

*Localities:* MANITOBA - abundant everywhere, at least south of Mile 214 Hudson's Bay Railway. MINNESOTA - probably generally distributed and abundant.

Genus *Colymbetes* Clairville

*Colymbetes longulus* LeConte. (2627)

*Localities:* MANITOBA - found sparingly on the western edge of the coniferous forests and very rarely further west.

*Collecting notes:* Most specimens have been collected from ponds in larch swamps. A few have been found elsewhere.

*Colymbetes dahuricus* Aubé

[Note. - A single female collected at Mile 214 Hudson's Bay Railway was assigned to this species; it probably belongs to the species *longulus* LeConte.]

*Colymbetes sculptilis* Harris complex. (2632)

[Note. - Wallis separates the Manitoba specimens into three species: *dolobratus* Paykull (Mile 474, Hudson's Bay Railway); *rugipennis* Sharp (widely distributed), and *sculptilis* Harris (widely distributed). According to Young and Severin (1956), the names *rugipennis* and *sculptilis* are synonyms. Also, Wallis' specimens of *dolobratus* probably represent a northern form of *sculptilis*.]

*Localities*: MANITOBA - widely distributed. MINNESOTA - widely distributed.

Genus *Dytiscus* Linnaeus*Dytiscus fasciventris* Say. (2636)

*Localities*: MANITOBA - throughout the southeast portion of the province. MINNESOTA - throughout the state.

*Dytiscus hybridus* Aubé. (2637)

*Localities*: MANITOBA - Southern portion. MINNESOTA - throughout the state.

*Dytiscus verticalis* Say. (2638)

*Localities*: MINNESOTA - common southward and eastward.

*Dytiscus sublimbatus* LeConte. (2640) (= *cordieri* Aubé)

*Localities*: MANITOBA - generally distributed in southern half, west of Canadian Shield. MINNESOTA - Hubbard Co., Norman Co., Ottertail Co., Pine City; St. Peter.

*Dytiscus anxius* Mannerheim.

*Localities*: MANITOBA - fairly common in southern portion.

*Dytiscus parvulus* Mannerheim. (2642)

*Localities*: MANITOBA - southward only, rather rare. MINNESOTA - Hubbard Co., Ramsey Co., St. Peter.

*Dytiscus dauricus* Gebler. (2645)

*Localities*: MANITOBA - Husavick, and southeastward; Winnipeg.

*Dytiscus harrisi* Kirby. (2646)

*Localities*: MANITOBA - in the southeast portion of the province. MINNESOTA - Isanti Co., Le Sueur Co., St. Anthony Park.

## SUBFAMILY HYDATICINAE

Genus *Hydaticus* Leach*Hydaticus modestus* Sharp.

*Localities*: MANITOBA - generally distributed. I have one specimen labelled H. B., but the species is not common north of Le Pas. MINNESOTA - generally distributed.

*Hydaticus piceus* LeConte. (2649)

*Localities*: MANITOBA - Victoria Beach and southeastward, Winnipeg. MINNESOTA - Albert Lea, Le Sueur Co., Ramsey Co., St. Paul.

Genus *Acilius* Leach*Acilius semisulcatus* Aubé. (2651)

*Localities*: MANITOBA - abundant in southern half. MINNESOTA - abundant throughout.

*Acilius fraternus* Harris. (2652)

*Localities*: MINNESOTA - Anoka Co., Becker Co., Grand Marais, Hibbing.

*Acilius mediatius* Say. (2653)

*Localities*: MINNESOTA - Ramsey Co.

Genus *Thermonectes* Crotch*Thermonectes ornatocollis* Aubé. (2654)*Localities:* MINNESOTA - Le Sueur Co. (Fish Hatchery).Genus *Graphoderus* Aubé.*Graphoderus liberus* Say. (2659)*Localities:* MANITOBA - in the southern half; local, not common. MINNESOTA - probably universally distributed.*Graphoderus perplexus* Sharp. (2661)*Localities:* MANITOBA - throughout southern half. MINNESOTA - Grand Marais, Ramsey Co., St. Louis Co., St. Paul.*Graphoderus fasciatocollis* Harris (= *fascicollis* Harris)*Localities:* MINNESOTA - Anoka Co., Beaver Dam, Hubbard Co., Le Sueur Co., Owatonna, Ramsey Co., Stillwater, St. Paul.*Graphoderus manitobensis* Wallis.*Localities:* MANITOBA - Winnipeg (single male type).*Graphoderus occidentalis* Horn. (2663)*Localities:* MANITOBA - abundant in southern portion. MINNESOTA - Grand Marais, Hubbard Co., Le Sueur Co., Ramsey Co., St. Anthony Park, St. Paul.

## SUBFAMILY CYBISTERINAE

Genus *Cybister* Curtis*Cybister fimbriolatus* Say. (2667)*Localities:* MINNESOTA - Le Sueur Co., St. Paul.

## FAMILY GYRINIDAE

Genus *Dineutus* MacLeay*Dineutus discolor* Aubé. (2674)*Localities:* MINNESOTA - Mora (one specimen).*Dineutus horni* Roberts. (2681)*Localities:* MINNESOTA - apparently throughout the state.*Dineutus nigrrior* Roberts. (2679)*Localities:* MANITOBA - Victoria Beach (one specimen). MINNESOTA - Ramsey Co., St. Louis Co., St. Paul.*Dineutus assimilis* Kirby.*Localities:* MANITOBA - southern half. MINNESOTA - universally distributed.Genus *Gyrinus* Geoffroy*Gyrinus minutus* Fabricius. (2684)*Localities:* MANITOBA - very abundant, north to Churchill. MINNESOTA - abundant throughout the state.*Gyrinus ventralis* Kirby. (2691)*Localities:* MINNESOTA - Ramsey Co.*Gyrinus aeneolus* LeConte. (2687)*Localities:* MANITOBA - Township 7 Range 11E. MINNESOTA - Anoka Co., Hennepin Co., Mora, Ramsey Co., Rochester.*Gyrinus dichrous* LeConte. (2689)*Localities:* MANITOBA - Berens River (east side of Lake Winnipeg). MINNESOTA - Afton, Detroit, Itasca State Park.

*Gyrinus latilimbus* Fall. (19250)

*Localities:* MINNESOTA - Bengall, Cook Co., Two Harbors.

*Gyrinus bifarius* Fall. (19251)

*Localities:* MANITOBA - not taken in southern half of the province; moderately abundant from Le Pas northward at least as far as the Kettle Rapids on the Nelson River. MINNESOTA - Mora (one specimen).

*Gyrinus confinis* LeConte. (2685)

*Localities:* MANITOBA - abundant everywhere as far north as the Kettle Rapids. MINNESOTA - Detroit, Itasca Co., Lake City, Lake Itasca.

*Gyrinus aquiris* LeConte. (2692)

*Localities:* MANITOBA - Husavick (one male). MINNESOTA - Detroit, Hennepin Co., Minneapolis, Ramsey Co., St. Paul.

*Gyrinus maculiventris* LeConte. (2695)

*Localities:* MANITOBA - extremely abundant as far north as Mile 214 Hudson's Bay Railway. MINNESOTA - apparently abundant, at least in northern half of state.

*Collecting notes:* This species remains active all winter, specimens having been taken at a hole in the ice on the Assiniboine River near Treesbank by E. Criddle on January 9, 1928.

*Gyrinus affinis* Aubé. (2696)

*Localities:* MANITOBA - widely distributed. MINNESOTA - Cook Co., Lake Co., Rawichami River, St. Louis.

*Gyrinus borealis* Aubé. (2707)

*Localities:* MANITOBA - recorded by Bell from the Nelson River 55° 50' N 99° 30' W, but I have no means of checking the record.

*Gyrinus pugionis* Fall. (19255)

*Localities:* MINNESOTA - Babbitt, near Ely, Itasca State Park.

*Gyrinus picipes* Aubé. (2704)

*Localities:* MANITOBA - Mile 214 Hudson's Bay Railway.

*Gyrinus lugens* LeConte. (2707a)

*Localities:* MANITOBA - widely distributed. MINNESOTA - Kawishiwi River, Lake Co.

*Gyrinus analis* Say. (2700)

*Localities:* MANITOBA - Onah (a single female det. by H.C.Fall). MINNESOTA - Fort Snelling, Minneapolis. Rochester.

*Gyrinus opacus* Sahlberg. (2702)

*Localities:* MANITOBA - Mile 214 Hudson's Bay Railway and northward.

*Gyrinus wallisi* Fall. (19256)

*Localities:* MANITOBA - Baldur, Stonewall, and northwards probably to the northern limits of the province.

*Gyrinus impressicollis* Kirby. (2706)

*Localities:* MANITOBA - Mile 214 Hudson's Bay Railway (Piquitenay River)

*Collecting notes:* In 1917 I took a few specimens on the Piquitenay River. These were swimming on the rough surface of the deeper water in ones or twos and were seen nowhere else. A few years later, a specimen or so turned up unexpectedly among some material taken in the evening when crossing Long Pine Lake at Ingolf, Ontario. The experience on the Piquitenay River was recalled and on my next visit to Ingolf search was made for *impressicollis* out in the deep waters some distance from shore, with such success that many were captured. This information was passed on to Mr. W. J. Brown of Ottawa who also took it in numbers on Lake Kazubazua, Quebec. Hence, it seems probable that if search be made in the rougher waters some distance from the shores, *impressicollis* will be found to inhabit most of the rocky lakes of the Laurentian Highland.



## ADDENDA

- Hydroporus lapponum* Gyllenhal. (19216)  
*Localities:* MANITOBA - Churchill (Brown, 1937).  
*Agabus browni* Leech  
*Localities:* MANITOBA - Churchill (Leech, 1938).  
*Agabus colymbus* Leech  
*Localities:* MANITOBA - Churchill (Leech, 1938).  
*Agabus hudsonicus* Leech  
*Localities:* MANITOBA - Churchill (Leech, 1938).  
*Agabus velox* Leech  
*Localities:* MANITOBA - Churchill (Leech, 1939).

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BIOLOGY OF *BOMBUS POLARIS* CURTIS AND *B. HYPERBOREUS* SCHÖNHERR  
AT LAKE HAZEN, NORTHWEST TERRITORIES  
(HYMENOPTERA: BOMBINI)

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*Adaptations for survival in a high arctic environment by Bombus polaris and B. hyperboreus are described. For B. polaris, adaptations related to low temperature are: structural characteristics of adults—large size, long dense hair, and dark color; behavioral—nest constructed on surface sites, with entrance facing towards the sun at maximum elevation, and flight by queens and workers close to ground surface. For the short season of growth, adaptations include: development of only a single brood of workers prior to production of sexual forms; eggs of first brood all laid in a single cell, and larvae fed collectively; extended foraging activity by queens and workers in continuous daylight; and acceptance by foragers of a wide variety of flowers. B. hyperboreus is a nest parasite of B. polaris. Adults of B. hyperboreus are similar to those of B. polaris in characteristics not associated with nesting. Shortening of the life cycle of B. hyperboreus was achieved by elimination of the worker caste.*

This paper reports studies of various aspects of the biology of *Bombus polaris* Curtis, 1835 and *B. hyperboreus* Schönherr, 1809. The purpose of these studies was to determine how these species have adapted to life in an arctic environment. Investigations were conducted at Lake Hazen (81° 49' N, 71° 18' W), Ellesmere Island, Northwest Territories, Canada, in the study area described by Savile (1964), from May 24 to August 20, 1967 and May 30 to August 28, 1968.

#### NOMENCLATURE, SYSTEMATICS AND GEOGRAPHICAL DISTRIBUTION

The high degree of polymorphism exhibited by northern species of *Bombus* and lack of communication between North American and European workers in describing new species collected by early arctic explorers has resulted in lengthy synonymies. Not all such problems are yet settled, and an explanation is required to justify use of one of the names in this paper.

Because the name *Bombus arcticus* Kirby, 1824, used by Richards (1931) is a secondary junior homonym of *Apis arctica* Quensel, 1802, which in turn is a junior subjective synonym of *Bombus agrorum* Fabricius, 1793, Kirby's *arcticus* must be replaced by another name. The name *Bombus polaris* Curtis, 1835, a junior subjective synonym of *B. arcticus* Kirby, is available, and is used here as the valid name. O. W. Richards (pers. comm., 1969) accepts this name change.

The species *B. polaris*, *B. hyperboreus* and five others belong to the subgenus *Alpinobombus* (Richards, 1931 and 1968). The group is in need of revision, a task rendered difficult by shortage of material and much variation in physical characteristics among the species. Members of *Alpinobombus* are confined to arctic and alpine tundra in the holarctic-

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region. They are found in the Alps, Arctic Europe, Asia, Greenland, Arctic America, and in the mountains of western North America as far south as Arizona. *Bombus polaris* (Fig. 1) and *B. hyperboreus* (Fig. 2) are arctic and probably circumpolar forms. The apparent gaps in their ranges in Siberia probably represent lack of collecting.

McAlpine (1964, 1965a) indicated that members of only a small number of insect species live in the northwest Queen Elizabeth Islands because of the environmental influences, and that these are extremely tolerant of "harsh" arctic conditions. This harshness of the environment probably excludes members of *Bombus* from some areas. Generally the distributions of *B. polaris* and *B. hyperboreus* are similar; *B. polaris* is recorded from areas where *B. hyperboreus* is absent (i.e. Quebec and Labrador), whereas *B. hyperboreus* is recorded only from areas where some other member (*B. balteatus* or *B. alpinus*) of the subgenus is also recorded. Chernov (1966) and Brinck and Wingstrand (1949, 1951) illustrate this point. The distribution of *B. polaris* and *B. hyperboreus* was determined from the literature and from specimens in the Canadian National Collection and my collection. Records are published by Strand (1905), Sladen (1919), Friese (1923a), Richards (1931), Hellén (1933), Braendegarrd, Henriksen, and Spärck (1935), Skorikov (1937), Henriksen (1937, 1939), Carpenter and Holm (1939), Brinck and Wingstrand (1949, 1951), Yarrow (1955), Savile (1959), Bruggeman (1958), Ander (1965), Chernov (1966), Swales (1966), and Mosquin and Martin (1967).

## NESTING

### Artificial domiciles

To obtain enough bumblebees to study populations, flight activities, nest temperatures, food preferences, and interspecific associations, attempts were made to attract queens to artificial domiciles placed in their natural habitats. Colonies established in artificial domiciles are easier to study than those in natural nests.

*Materials and methods.* - I used light weight domiciles of two designs (Fig. 3), each including three parts: a masonite base, a body with entrance hole 19 mm or 25 mm diameter, and a styrofoam top. Tops of one type were inverted blue flower pots, and bodies were pieces of 15 mm shellac-soaked cardboard tubing. Tops of the second type were rectangular white boxes on bodies of ¼ in. plywood. Nesting material of upholsterer's cotton was placed inside each box. Entrance directions varied. Black polyethylene tubing, one foot long, of either 22 mm or 13 mm outside diameter, was connected to the entrance holes of some domiciles to form entrance tunnels. The outer ends were cut obliquely to form landing platforms. Domiciles were placed on the ground with small pebbles, soil, vascular plants and moss over the tunnels. Permafrost barred the use of underground nests. In 1967 200 domiciles in 10 localities and in 1968 180 domiciles in nine localities were used. The domiciles were placed in the field when spring melt commenced. Because many domiciles were damaged by arctic foxes, arctic hares, and musk oxen, fine-mesh chicken wire was secured over the tops of the accepted domiciles to protect them.

*Results.* - Of the 380 domiciles used in two years, only five were occupied by *B. polaris* queens. Each was of the blue styrofoam flower pot type with a large tunnel. Entrances to three faced between 250° -280° and two faced between 100° -115° range, suggesting no strong directional preference by the bumblebees which occupied them. The domiciles were in four different habitats. At acceptance time, adjacent areas were free of snow, though some melting snow drifts remained on N and NE-facing banks of Skeleton Creek and on slopes in the higher fault zone.

## Natural nests

The purpose of this investigation was to discover factors controlling nest initiation by arctic bumblebees. Areas that queens rejected while searching and the habitats in which they eventually established were also investigated.

In the arctic regions, data about nests of various *Alpinobombus* species have been reported by: Jacobson (1898), Friese (1904, 1908, 1923a, and b), Johansen and Nielsen (1910), Frison (1919), Friese and Wagner (1912), Sladen (1919), Brinck and Wingstrand (1951), Freuchen and Salomonsen (1958), Løken (1961), and Milliron and Oliver (1966).

*Materials and methods.* -Queens in search of nesting sites were observed, and these data were recorded: amount of time spent searching, habitats and sites investigated, possible reasons for rejection of particular sites, temperatures and moisture conditions of the soil, available nesting material, and directions of tunnel entrances. Each queen in natural and artificial domicile nests was marked with nail polish on a particular part of the body as soon as the nest was found so that she could be recognized again.

Date of nest establishment was calculated by subtracting one to six days from the date on which the nest was discovered, depending upon kind and amount of progress at the time (Hobbs, 1964b). Data from the accepted artificial domiciles are included to indicate peaks of establishment.

*Areas in which nests occur.* -Of 94 natural nests located at Lake Hazen, 92 were on the surface of the ground, one was on a caribou rug in the sleeping tent, and one was in an abandoned lemming burrow. Nests were in marsh and sedge meadows along streams (Skeleton Creek and creek no. 51) and beside pools and tarns (i.e. those in T6, Q7, P6, M10 of Fig. 6). Three nests described by Milliron and Oliver (1966) were also in marsh meadows.

General characteristics and vegetation of marsh and sedge meadows (Fig. 7) and marginal areas around each of the pools and tarns have been described by Savile (1964) and Oliver and Corbet (1966). Plants found<sup>1</sup> in the moister meadows are of *Juncus albescens* (Lge) Fern., *J. castaneus* Sm., *J. biglumis* L., *Eutrema edwardsii* R. Br., *Cardamine pratensis* L., *Saxifraga hirculus* L., and *Ranunculus trichophyllus* Chaix. The principal mosses are *Drepanocladus brevifolius* (Lindb.) Warst and *Bryum* spp. The drier meadow areas are characterized by the dominant *Carex aquatilis* Wahlenb. var *stans* (Drej.) Boot. with varying amounts of *Eriophorum scheutzeri* Hoppe, *E. triste* (Th. Fries.) Hadac and Løve, *J. biglumis*, *Arctagrostis latifolia* (R. Br.) Griseb., *Polygonum viviparum* L., *Salix arctica* Pall. and lesser amounts of *Equisetum arvense* L., *E. variegatum* Schlecht., *Pedicularis arctica* R. Br., *P. hirsuta* L., *Cerastium beeringianum* Cham. and Schlecht., *Saxifraga nivalis* L., *S. rivularis* L., and *Ranunculus sulphureus* Sd. The principal bryophytes are *Drepanocladus revolvens* (Sw.) Warnst, *Orothecium chryseum* (Schultes) BSG., and *Campylium arcticum* (Williams) Broth., and *Bryum* spp. The vegetation forms a closed cover over the partly decaying organic material (Day 1964).

In meadows and marginal pool areas natural nests were on small flat areas, in depressions, and beside small hummocks of moss or other vegetation. Variations in structure were numerous. The majority ( $P > 0.005$ ) of nests (Fig. 5a) examined had entrances which faced in the 180° to 270° quadrant; more (Fig. 5b) faced between 225° and 270° than in the 180°-225° sector. A possible explanation is the sun orientation at the daily temperature peak. The maximum diel soil surface temperature occurred between 1300 and 1600 hours (Corbet 1966, 1967a, b) when the bearing of the sun progresses from 195° to 240°. The highest temperatures around a conical mound of moist moss were at the west, not at the south where the sun's altitude was greatest: surface temperature of the north slope remained almost steady through 24 hours. Also, moss mounds and *Dryas* hummocks in sedge meadows

<sup>1</sup> Throughout the text, flower nomenclature follows that of Porsild (1964) and Savile (1964) and bryophyte nomenclature is that of Brassard (pers. comm. 1969).]

were the warmest areas and showed exceptionally marked diel periodicities of surface temperatures (Corbet, 1967b). Moderate to light moisture conditions were not deterrent factors in nest establishment for though the nests often became waterlogged beneath they remained comparatively dry on the surface. Nests in the sedge meadows and along the north banks of the streams were drier; the moisture in and around these nests resulted from the later permafrost melt.

In an attempt to discover why surface sites in meadows and marshes were preferred to rodent burrows (the traditional sites of bumblebee nests in temperate areas), temperature data were obtained for both types of sites. Data are presented in Table 1 for abandoned lemming holes at least 30 cm deep which queens had investigated. In a marsh and sedge meadow (M7, Fig. 6) 75 readings were recorded from a grid 25 meters long by eight meters wide (Table 2). Temperatures at the soil surface fluctuate daily, especially during June at Lake Hazen (Powell, 1961; Corbet, 1967b) which may influence the temperature of the marsh and sedge meadows. Soil temperatures measured one foot beneath the surface (Powell, 1961) were lower than temperatures in lemming burrows. The latter were more exposed and more influenced by surface temperatures and solar radiation. Nonetheless, temperatures in the lemming burrows were lower than those in the marsh meadow.

Table 1. Temperatures in abandoned lemming holes when they were investigated by *B. polaris* queens; June 3 to June 23, 1967, and June 15 to July 3, 1968, at Lake Hazen, N. W. T.

	Number of lemming holes investigated	Range	Temperature, °C	
			Mean	SD
1967	26	-1.1 to +3.9	1.20	0.98
1968	39	-1.8 to +2.8	0.64	0.73

Table 2. Soil temperature ranges at 5 cm depth in a marsh and sedge meadow (M7, Fig. 6) at 1400 hrs. on three different days in 1968 at Lake Hazen, N.W.T.

	Air temp 15 cm above ground		Soil Temperature, °C at 5 cm		
		N	Range	Mean	SD
June 17	7.5	75	0.7- 7.0	4.82	1.10
June 25	11.0	75	1.5- 8.5	6.35	1.28
July 2	9.5	75	3.0-12.0	8.28	1.58

Moisture conditions of the burrows examined by queens were also investigated. About 75 per cent of the burrows contained ice or permafrost, or were extremely damp in some part. In contrast, surface moss and liverworts of the marsh meadows were not so affected by ice and permafrost, although they were briefly inundated by the fluctuating water level during snow melt. In summary, surface areas of marsh and sedge meadows were warmer and drier than were most of the lemming burrows.

*Emergence of queens and the search for nest sites.* - Physiological factors associated with egg development probably stimulate a queen to seek a nest and start a colony (Medler 1962a). The ovaries of *B. (Bombus) lucorum* L. queens in Surrey, England did not develop until after a hibernation period (Cumber 1949) followed by an active feeding period of almost three weeks resulting in a noticeable increase in weight and in a swelling of the ovarioles (Cumber 1949, 1953). At Hazen the pre-feeding period is about a week. After their ovaries mature the *B. polaris* queens search for nesting sites.

The first *B. polaris* queens were observed May 27, 1967 and June 14, 1968, and the first *B. hyperboreus* queens were observed on June 9, 1967 and June 21, 1968. During the first few days of the season, queens visited for nectar and pollen the flowers of *Saxifraga oppositifolia*, the only ones in bloom at the time.

Hunting begins when *Salix arctica* blooms, which is within a week after the first flowers of *Saxifraga oppositifolia* appear. In 1967, searching by *B. polaris* queens extended from June 3 to June 23, and in 1968 from June 15 to July 3. Searching for nests of *B. polaris* by queens of *B. hyperboreus* extended from June 15 to July 16 in 1967, and from June 23 to July 10 in 1968. Searching by *B. polaris* queens reached a peak four to six days after beginning and then declined for the rest of the period. For example, on June 19, 1968, 24 *B. polaris* queens were observed seeking nests, whereas on June 30, only two such queens were observed. The activity of *B. hyperboreus* queens reached a peak seven to 11 days after they became active.

Queens searched in cracks in the soil in clay banked areas, in rocky areas, in marsh and sedge meadows, around *Dryas* hummocks, and in abandoned burrows of lemmings. They even searched the walls and caribou rug floors of the tents. Queens flew throughout the 24 hour period if the weather was favorable, usually less than 25 cm and not more than 30 cm above ground level. They alighted now and then to inspect promising sites more closely.

The lemming burrows investigated were usually those with south to northwest-facing entrances (Fig. 4). Diameters of these tunnels were in the 4-8 cm range. Investigation of a burrow usually occupied less than 30 seconds, but some queens spent up to three minutes in this activity.

Suitable material for construction of bumblebee nests was found in 27 lemming burrows. This material had probably been used in construction of lemming nests and included dried or decaying grasses, sedges, mosses hair, and feathers. Marsh meadows also provided nesting material of mosses, leaves, grasses and sedges. Suitable nesting material was absent from sparsely vegetated areas of saline clay, sand, gravel, *Dryas-Kobresia* habitats, mud and gravel deltas, and most *Dryas* hummock habitats.

Nest establishment for nine *B. polaris* queens observed began on June 7 and ended June 17, 1967. The peak occurred June 9 or June 10 when four of the queens established. In 1968, for eight queens, the period was from June 15 to 25 with no obvious peak. Three queens, while in the process of establishing, abandoned their nests, apparently because of disturbances during examination. Four queens failed to return to their nests after a light snow storm on June 29, 1968 when the screen temperature was 1.0 C.

*Nest construction.* -Upon accepting a suitable location to establish a natural nest (Fig. 7) or occupy a domicile, a queen completely rearranges the nesting material to form a brood chamber. To loosen and rearrange the moss she pulls it with her mandibles and fore-legs and pushes it under her body to the desired position with her mid- and hind-legs. Queens (and later, assisting workers), continue to rearrange the material so long as the colony is expanding. Most nesting material consists of mosses and liverworts. Names of the principal bryophytes from 92 nests are presented in Table 3. The principal vascular plant-nesting material consisted of dried blades of *Carex aquatilis* and *Eriophorum* spp. with *Equisetum* spp., *Dryas* and *Salix* in some nests. For a complete list of mosses and liverworts from the nests with relative abundance, see Richards (1970). In 1967, representatives of 46 mosses and four liverworts with an average of 7.1 (range 2-14) species were collected from each of the nests; in 1968, representatives of 48 mosses and eight liverworts with an average of 6.7 (range 3-13) species per nest were collected.

Table 3. The principal bryophytes from 92 natural nests of *B. polaris* at Lake Hazen, 1967, 1968.

	Number of nests with moss	
	1967	1968
<i>Barbula icmadophila</i> Schimp ex Mull	10	5
<i>Bryum</i> spp.	38	33
<i>Calliergon giganteum</i> Schimp (Kindb)	11	14
<i>Campylium arcticum</i> (Williams) Broth.	36	25
<i>Cirriphyllum cirrosum</i> (Schultes) Grout	13	1
<i>Distichium capillaceum</i> (Hedw.) BSQ	21	19
<i>Distichium</i> sp.	10	5
<i>Ditrichum flexicoule</i> (Schwacgar.) Hampe	19	19
<i>Drepanocladus aduncus</i> (Hedw.) Warnst.	14	8
<i>Drepanocladus revolvens</i> (Sw.) Warnst.	20	28
<i>Orthothecium chryseum</i> (Schultes) BSG	24	29
<i>Tomenthyonum nitens</i> (Hedw.) Loeske	12	10

Nests changed as the season progressed. Earlier the external dimensions were small, about 5 cm diameter, whereas later some were as large as 15 cm. The external covering of the nest cavity was convex-oval with the mosses and dried sedge leaves intermixed to form a thick and tightly constructed surface. The covering of some nests reached a height of 5 cm. Nest cavities were in shallow depressions covered with dried moss, leaves, roots and occasionally peat. The queen and workers excavated parts of the moss mounds beside the nests where the bees defecated.



**Discussion.-** The factors controlling nest initiation are complex. Whatever physiological factors are involved must take effect either promptly after emergence from hibernation or become effective during the fall feeding period and then again before or during spring emergence. Queens investigate all major habitats for a suitable site. That queens search such areas as lemming holes suggests that in some localities *B. polaris* queens regularly establish underground. This is also suggested by a few publications (Johansen and Nielsen, 1910; Frison, 1919). Another possibility is that underground searching is a trait inherited from the ancestral stock of *B. polaris*.

The habitat in which the queen establishes her nest has the following characteristics; it is warmer than habitats of compact soil, has more suitable nesting material than is present in *Dryas-Kobresia* habitats, or in sand and gravel knoll habitats; it is adjacent to food sources; and it lacks the excessive moisture of the clay, sand, gravel, and *Dryas* hummock areas during nest establishment. I believe that low temperatures of soil or lemming burrows inhibit queens from establishing in such places, even if other factors are favorable. While founding queens are not specific in choosing nesting material, they seem to prefer leaves and bracts of mosses and liverworts.

Interestingly, queens investigated lemming burrows with entrances facing the same direction as sites on which most nests were located. The patterns of distribution and behavior of bumblebees are correlated with the aspect of the slope they inhabit, as is true of many other organisms living in the arctic environment (Corbet, 1967).

## COLONY DEVELOPMENT

### Colony composition

Among the potential aspects for adaptations of arctic and alpine bumblebees are the physiological and morphological stages of a colony. Because the climatic environmental factors (i.e. low temperature, small heat budget, and reduced growing season) are more severe than in other regions the adaptive developmental changes have become vital in allowing the bumblebees to survive in the high arctic.

There has been little previous work on *Alpinobombus* brood-rearing behavior and all but two of the authors who have investigated the various species, described only the contents of nests at a particular stage when they were collected (Sladen (1919); Frison (1919 and 1927a); Brinck and Wingstrand (1951); Johansen and Nielsen (1910); Milliron and Oliver (1966); Hasselrot (1960); Hobbs (1964a and b); Løken (1961)).

**Materials and methods.-** Observations and rough sketches were made and photographs were taken of five artificial domicile nests and 24 natural nests at intervals of two to five days throughout the seasons. I determined arrangement and number of eggs, larvae, pupae, and pollen by dissecting the wax-pollen canopy covering the broods. Nests were periodically collected and the brood was examined in the laboratory.

Before I gained experience in removing the protective covering and accidentally touched the brood, the workers removed the eggs or larvae from a recently exposed wax-pollen cell with their mandibles and carried them outside the nest. These larvae were examined and collected. I also observed workers eating the exposed eggs in egg cups an activity which led Brian (1951) to suggest cannibalism. When I exercised care and did not touch the eggs or larvae, the workers repaired the wax-pollen covering over them. During observations, exposure of the nest resulted in temperature drops comparable with those resulting from absence of a queen during foraging (Fig. 17); such additional cooling is not considered to be an important stress factor on brood development. In one instance, a 15 minute observation resulted in a drop in nest temperature of 8.25 C (30.25 to 22 C), in another, a 17 minute observa-

tion resulted in a decline of 10.0 C (31 to 21 C).

*First brood.*- The following is a summary of observations: After a queen of *B. polaris* completely rearranges the moss or upholsterer's cotton nesting material, she visits flowers of *Saxifraga oppositifolia* or *Salix arctica* and returns to the nest with two pollen pellets. After placing these pellets side by side she builds the wax-pollen first brood cell (Fig. 8) on top of them. The honey pot was built after the brood cell by the nine queens observed. The honey pot is built separately from the brood and in line with the longitudinal axis of the incubation groove. It is sufficiently near the groove that the queen while incubating drinks from it without leaving the brood. Before she builds the honey pot the queen stores honey in the moss and cotton nesting material, providing a small food reserve which also acts as an early insulating layer. Eggs are usually deposited vertically in a single cup, at one time. In one instance the egg cell was probably reopened and additional eggs were laid, for they were in two separate groups within the cell. Egg cells have a definite area under them for fresh moist pollen during larval development. Thus the queen at this stage is a "pocket-maker". The wax-pollen canopy covering the egg cells is a dark brown, rough mass colored by the yellowish pollen of *S. oppositifolia* and *S. arctica*. The incubation groove, although poorly formed on the egg cell, was present in all nests observed.

First brood larvae are fed moist, easily manipulated pollen by the queen. She pushes it under the brood in several places, especially under the sides of the incubation groove. Larvae in front of the incubation groove (toward the nest entrance) were larger and developed more rapidly than those toward the back, because most pollen is pushed under larvae in the former position and the honey pot is nearer to them. After one to three days growth, the larvae lie side by side in a curled position (Fig. 9) allowing easy access to the pollen below. When pollen is plentiful the larvae eat into the mass until they become completely enclosed. Last instar larvae construct separate cells immediately before spinning cocoons and are then fed individually with a mixture of honey and pollen. Often they are such a size that the wax-pollen canopy does not completely cover them. In some nests the color of the wax-pollen covering first the egg cells and then the larvae changes from a dark brown to a lighter tan, owing to a change in the pollen supply.

Cocoons are separated from each other by flimsily spun silk and by the wax-pollen covering. When no fresh pollen is brought into the nest, that already present begins to harden and dry. The incubation groove, evident from the initial egg cell construction, is more pronounced from mid-larval stage to worker emergence.

First brood larvae usually become workers. In one instance, however, three workers and 11 males (imagines and late pupae) were present when a nest was collected. This nest was still developing, for it had an egg cell with 12 eggs and eight two-or-three-day old larvae. The queen had abandoned the nest, apparently because there were fewer workers to assist her in food gathering and incubation, and the few emerged males and workers had depleted the honey. The workers which emerge first are those in the front of the brood nearest the honey pot on the base of the incubation groove. Succeeding emergences progress posteriorly through the incubation groove to the brood furthest from the honey pot. Hence the larger workers emerge first, the small ones later. Marked variation in size of workers within one nest has been reported for other species by Sladen (1912), Cumber (1949), and Medler (1962b, 1965).

*Second and third broods (sexuals).*- Second and third brood egg cells, also made of wax-pollen material, are built on the outside tops of the cocoons that form the sides of the incubation grooves (Fig. 10). The egg cells are constructed one to two days before or after the first brood larvae begin to spin. Eggs at this time are laid in a horizontal orientation (Figs. 11, 12), with most side by side or on top of each other. In 10 of 13 instances, the

first eggs were placed in the egg cell which occupied the front half of the incubation groove. Usually, one of the ridges of an incubation groove was completely covered with egg cells before any were built on the other ridge. Additional egg cells were not built on the same ridge, until after the first eggs had hatched. As a result, brood in different stages of development can be on the same ridge. No pollen is placed in or under the egg cells to prime the eggs of the second or third broods. The egg cells are small, thick, dark brown wax-pollen cups 6-7 mm long and 3-4 mm wide according to the number of eggs laid in them.

When larvae on the fore part of the incubation groove emerge the wax-pollen canopy covering is not extended to any adjacent or posterior group. Therefore, the larvae beneath the canopy on any ridge are separated and of different sizes on each side of the incubation groove. Fresh moist pollen is pushed into pollen pockets (Fig. 13) beneath the larvae on the edges of the brood when the first eggs hatch. The pollen pots for feeding male and queen larvae are larger than the pollen receptacles under the worker larvae. Bees at this stage of development become "pollen storers." The curled position and pollen diet of second and third brood larvae are identical to those of first brood larvae. Although they built separate cells the last instar larvae were not always completely covered with wax as were the earlier instars. All larvae are fed pollen; larvae of sexuals are also fed honey from the honey pots. Last instar larvae are fed by workers through holes in the wax-pollen canopies.

While the first male cocoons were being spun (Fig. 14), egg cells were still being built; eggs in these cells either did not develop or they were removed by workers. None of the second or third brood in any observed nests were workers. The first egg batches of the sexual brood produced males. Subsequent batches, laid on the remaining part of the incubation groove or on the canopy covering the last instar larvae and early cocoons of the second brood, produced queens (Fig. 15). Males remained in the nest up to two days whereas the queens remained up to seven. The original established queen remained with her nest until after the first males emerged.

*Honey pots.*- Queens built two or three additional honey pots up to 2-3 cm high and 1-1.5 cm diameter before the workers emerged. These were usually  $\frac{1}{2}$  to  $\frac{3}{4}$  full. During the season the capacity of each honey pot varied, as first the queen and later the workers added or removed wax. Two small honey pots, one taken from each of two nests while the first brood was in the egg stage, had capacities of 1.12 cc and 1.73 cc. After the workers emerged, as many as 14 honey pots were built (Fig. 16), each usually  $\frac{1}{2}$  to  $\frac{3}{4}$  full of honey, less full in times of unfavorable weather. Honey was also stored in some of the old worker cocoons and the empty male cocoons, but these storage areas were at most  $\frac{1}{4}$  full.

*Population structure.*- The population of eggs, larvae, and pupae of the first, second, and third broods for each year are indicated in Table 4. Reasons for the variation in egg numbers are unknown. The ratio in spring of females to workers produced was 1:16, and in fall the ratio was 1:3.03 (1967) and 1:1.76 (1968). The numbers of eggs per cell of male and female broods is given in Table 5. Differences in numbers between years and in sex ratio were not statistically significant at the 95% level. The ratio of the number of larvae of sexual forms to the number of workers in 1967 was 1.57; in 1968 it was 1.53. Sex ratios within each nest were in 1967, 2.0 males per female and in 1968, 1.6 males per female. Although queens were successful in rearing almost all first brood workers to maturity, they were less successful with second and third broods. Of those nests studied during the entire seasons of 1967 and 1968, mortality before emergence of adult males was 57.1% and 37.2% and of adult females was 62.5% and 41.0%.

Table 4. Numbers of first, second, and third broods of eggs, larvae, and pupae from nests of *B. polaris* at Lake Hazen, N.W.T., for 1967 and 1968.

	First brood (worker)		Second brood (male)		Third brood (queen)	
	N	Range	N	Range	N	Range
1967						
Egg	2	16-17	8	4-34	8	8-23
Larvae	6	14-17	7	4-23	8	2-18
Pupae	8	13-17	5	2-15	5	2- 6
1968						
Egg	2	15-17	6	6-24	6	11-18
Larvae	7	15-17	8	8-24	7	3-16
Pupae	6	14-19	7	4-24	5	5-16

Table 5. The numbers of eggs per egg cell of *B. polaris* male and female broods per year in the artificial domicile nests and natural nests at Lake Hazen, N.W.T.

	Male		Female	
	N	Range	N	Range
1967	21	2-13	18	4-17
1968	11	3-14	10	5-12

Times required for development of each stage and each brood of *B. polaris* for each year, are given in Table 6.

*Discussion.*- Species of *Alpinobombus* differ from one another and from members of other subgenera in oviposition characteristics, colony size, brood composition, and length of time required to complete stages of the life cycle. As an illustration of subgeneric differences, data for *B. balteatus* (Hobbs, 1964a, b) are aligned with my data for *B. polaris* (Table 7).

Table 6. Duration of development in days of eggs, larvae, and pupae of first, second, and third broods of *B. polaris* at Lake Hazen, N.W.T., 1967 and 1968

	First brood (worker)		Second brood (male)		Third brood (queen)	
	N	Range	N	Range	N	Range
1967						
Egg	5	3.5-4	7	3.5-4	7	3.5-4
Larvae	9	7.0-9	3	9.0-11	4	7.0-9
Pupae	8	7.0-9	3	7.0-11	4	9.0-11
Total (egg-adult)		17.5-22		19.5-26		19.5-24
1968						
Egg	1	3.5-4	3	3.5-4	2	3.5-4
Larvae	3	7.0-8	3	7.0-9	2	6.0-8
Pupae	4	6.0-11	4	9.0-14	5	9.0-13
Total (egg-adult)		16.5-23		19.5-27		18.5-25

Table 7. Differences between the composition and development of brood of *B. polaris* and *B. balteatus* (data for *B. balteatus* after Hobbs 1964b).

*B. polaris*

*B. balteatus*

First brood

- all eggs deposited at one time
- average no. of eggs in four broods 16.24 (range 15 - 17)
- average no. of larvae in 13 broods 15.9 (range 14 - 19)

- not all eggs deposited at one time
- average no. of eggs in eight broods 11 (range 7 - 21)
- average no. of larvae in five broods 14 (range 12 - 15)

Sexual brood

- eggs laid on same ridge of incubation groove were of different ages and castes
- wax-pollen canopy covering larvae of adjacent cells not extended to cover all larvae on the same ridge
- only one brood of workers produced before males and queens

- eggs laid on same ridge of incubation groove were of different ages but same caste
- wax-pollen canopy covering larvae of adjacent cells extended to cover all larvae on the same ridge
- sometimes more than one brood of workers produced before males and queens

Queens of *Alpinobombus* colonies are the only bumblebees known to place all eggs of the first broods in single egg cells. The numbers of eggs laid per cell for second and third broods of *B. polaris* (and probably for other species of *Alpinobombus*) were the same as those laid in succeeding worker and sexual cells by queens of the subgenera *Bombus* and *Cullumanobombus*, and were greater than the numbers laid by queens of *Subterraneobombus*, *Fervidobombus*, *Pyrobombus* and *Bombias*. The last-named is the only subgenus known of which queens lay only a single egg per cell for the second and succeeding broods (Hobbs, 1964a, 1965a).

More eggs per brood are laid by queens of *B. polaris* in the first three broods than are laid by queens of most other species of bumblebees. However, because of environmental factors restricting total number of broods, seasonal egg production overall is less for arctic species than for those inhabiting warmer areas, farther south.

Colonies of *Alpinobombus* species produced more workers in the first broods than did colonies representing most other sub-genera studied by Hobbs (1964-1968). It is difficult to estimate values for workers per queen in fall for species with colonies living under warmer conditions in lower latitudes because of the wide variation in numbers of workers among different colonies. Generally, however, values for this ratio are about the same for both temperate and arctic-alpine species.

Colonies of *Alpinobombus* species are small because usually only a single brood of workers is produced before a queen begins to produce the sexual broods (Hobbs, 1964a). Queens of other subgenera produce at least two worker broods—hence more workers— than *Alpinobombus* colonies produce. Among other subgenera, limited data suggest that number of workers per colony varies with latitude: the Holarctic arctic-alpine *B. (Pyrobombus) sylvicola* Kirby has as many as 139 worker cocoons (Hobbs, 1967b), whereas the tropical *B. medius* produces as many as 2183 workers (Michener and La Berge, 1954).

The paucity of workers led Friese (1902, 1908, 1923a and b) and Friese and Wagner (1912) to suggest that arctic bumblebees including *Alpinobombus* species are tending toward a solitary mode of life. I do not believe that this is so. Rather, I think that the reduced colony size is adaptive to life under arctic conditions. Certainly, queens of these northern taxa behave toward their broods as social insects, just as do their southern counterparts.

Hasselrot (1960) reported that rates of development of the various life stages and larval instars of a selection of *Bombus* species were similar to one another. Mean values for all species studied were as follows: egg stage - 3.4 days; larval stage - 10.8 days; pupal stage - 11.3 days; total average time of development - 24.5 days. The rate of development is comparable to the above data for the life stages of *B. polaris* (cf. Table 6).

Brood reduction in the form of mortality of immatures of *B. polaris* at Lake Hazen was the result of cannibalism and lack of food. The latter is related to periods of unfavorable weather (about 4.0 C to 2.0 C, wind 8-12 mph, and complete cloud cover) during which workers had difficulty in foraging and the food supply within the colonies became depleted (i.e. honey pots less than 1/3 full and scarcity of fresh moist pollen). Under these conditions, workers demolished egg cups and eggs and removed larvae from the nest, thus probably killing them. Food sources were also influenced by unfavorable weather as nectar secretion was reduced and stamens became devoid of pollen.

Mortality data for the observed colonies of *B. polaris* are insufficient for detailed analysis because not all second and third brood egg cells were opened to determine the maximum number of eggs laid. However, the data available suggest that colonies in artificial domiciles had fewer deaths than had colonies in natural nests, possibly because of the insulating effect of the styrofoam tops. Cumber (1949) estimates at least 50% mortality before emergence of

adults for bumblebees in general, and Brian (1951) estimates mortality of *B. agrorum* Fabricius colonies based on all broods except the last, for two years, at 64 and 69 per cent.

At Lake Hazen, bumblebees are one of the few groups of insects to use most of the period of active growth. Adults are active soon after the first flowers bloom in June, continuing until early in August when few flowers are left. Progression of brood development parallels progression of weather and plants.

### Flight activity

This is a sensitive indicator of foraging conditions in the field, and of the ability of colonies to exploit available food sources. Rate of food acquisition strongly influences reproductive capacity, and tempo of most activities within colonies of honey bees (Gary 1967), and the same principles may be applied to bumblebee flight activity. The purpose of this study was to characterize weather conditions affecting the foraging of arctic bumblebees, adaptations of the bees to the weather conditions, frequency of flight per 24 hours, and type of food (pollen or nectar) exploited.

The effect of weather and general climatic conditions on bumblebee flight is important, especially in arctic areas, where continuous daylight during the summer permits maximum frequency and duration of this activity (Jacobson 1898 in Friese 1904, 1908, 1923a, b, and Friese and Wagner 1912; and Johansen and Nielsen 1910; Sladen 1919; Frison 1919; Løken 1949, 1954; Longstaff 1932; Bruggeman 1958; Freuchen and Salomonsen 1958; Savile 1959; Hasselrot 1960; Gavrilov 1961; Downes 1964; Hocking and Sharplin 1964; and Milliron and Oliver 1966). Structural features of possible adaptive significance, such as large size, hairiness, and melanism, and some physiological factors affecting foraging in cooler weather are discussed.

*Materials and methods.*—In 1968, 24 hour observations were made every six days for 36 days at an artificial domicile. These six series of observations were made at the following six stages of development: (1) first brood mid-larval; (2) first brood early-pupal and second brood egg; (3) first brood emergence, second brood late-larval to early pupal, third brood egg; (4) second brood late-pupal, third brood mid-larval; (5) second brood early emergence, third brood pupal; and (6) third brood late-pupal to early emergence. Six supporting series of observations from a natural nest at unspecified intervals of hour and day, and occasional flight activity observations at an artificial domicile in 1967 were also made. The brood composition and population of the nests were recorded the day before each observation. Thus, the flight activity of bumblebees at major brood development periods was characterized.

Flight was observed from a seated position far enough from a nest to avoid disturbing the bees but near enough to recognize the caste (queen or worker) and presence or absence of pollen on legs. When reference is made to 'pollen load' or 'pollen-gathering' it is assumed that a bumblebee was often also carrying nectar (Brian 1952; Free 1955b). The terms 'nectar load' and 'nectar-gathering' are used only when the forager in question has not been gathering pollen (Free 1955b). For each flight the times (Eastern Standard) of departure and return, the caste of the bee and whether it carried pollen, were recorded. Air temperature was taken initially with a thermistor probe and later with a dial thermometer. Wind velocity in mph and wind direction were estimated with a portable floating ball-type anemometer. All were taken near the nest at a height above ground of 20-30 cm. Cloud cover was estimated visually. Several readings of air temperature, wind velocity and direction, and several estimates of cloud cover throughout each hour of observation were averaged to increase reliability of the data. Solar altitude was taken from Corbet (1966).

For each bee observed away from the nest entrance the following notes were taken: species, caste or sex, time, air temperature, flying height above ground, wind direction and ve-

locity at this height, and cloud cover.

*Frequency of food collecting at the nest entrance.*- The integral components affecting flight activity were the responses of foraging bees to intra-nest stimuli and to meteorological conditions. Various combinations of light, temperature, wind, and humidity affected bumblebee flight, and might be sufficient to bring about periodicities in flight. Thus, diel periodicities of weather factors near the ground at Lake Hazen (Corbet 1966, 1967b) are considered (Table 8). Jackson (1959a, b) reported for Lake Hazen that for 76% of the observations the average wind velocity from June 1 to August 2 was 5 mph or less. The predominant wind direction was NE, along the Lake Hazen trough (Jackson 1959b, 1960; Corbet 1966, 1967b) followed by ENE, E, and NNE (Corbet 1966). Cloud cover did not exhibit diel periodicity, but a tendency was noted for opacity to increase slightly between 1300 and 2200 hours (Corbet 1966).

Many of the diel fluctuations were obscured by weather trends persisting longer than a day, such as barometric pressure, wind velocity, and cloud cover. The most regular are those resulting directly from solar radiation at or near the soil surface (Corbet 1966).

Table 8. Diel ranges of times of maxima and minima of weather factors near the ground at Lake Hazen, N.W.T. (after Corbet 1966).

Weather factor	Maximum	Minimum
Solar altitude and short wave radiation	1000-1600	2200-0200
Soil-surface temperature	1300-1600	0100-0300
Stevenson screen temperature	1300-1900	0100-0700
Relative humidity	0100-0700	1300-1900
Wind velocity (at 41 feet)	1900-2200	1600-1900

The frequency of flight and the number of pollen and nectar loads collected on various days by foragers of *B. polaris* from an artificial domicile are shown in Figs. 17-22 and those for a natural nest are shown in Figs. 23-26.

Before workers emerged, the queen (Fig. 17) flew at all hours with approximately equal frequency, collecting more pollen than nectar to feed the first brood larvae. The queen was absent from the nest approximately 30 minutes on each of 20 foraging trips. After each forage she deposited pollen and nectar into pollen pocket(s) and/or honey pot(s) and warmed the brood to a temperature comparable to that of the nest before her forage. When the first brood was in the early pupal stage (Fig. 18) the queen collected pollen, but the frequency of her flights was less than during larval development.

The climax of worker foraging activity occurred between July 6 and July 16 when nutritional requirements of second and third brood larvae were maximal (Fig. 19 and Fig. 20). These larvae were fed mixtures of pollen and nectar. The proportions of pollen loads to nectar loads collected by foragers for these two days were 2.20:1 and 1.14:1 respectively. Thus, there is perhaps a difference in the proportions of pollen to nectar fed to the second and third brood larvae. Throughout July 6 the amount of pollen foraged remained nearly the same, whereas nectar gathering reached a peak during 1200 to 1600 hours. On July 12,



however, the pollen gathering peak was between 1000 and 1400 hours and nectar-gathering was proportionately higher most other times. Collectively nectar- and pollen-gathering occurred between 1200 and 1600 hours on July 6 and between 0900 and 1500 hours on July 12. The highest number of worker bumblebees (37) passing through the nest entrance in one hour was counted at about 1400 hours on July 6. On July 12 workers flew until 2330 and no foragers spent the night away from the nest.

The queen and workers foraged primarily for nectar when adults of the second brood began to emerge and during the third brood pupal period (Fig. 21). This corresponds to increase in number of honey pots, to feeding of second and third brood larvae quantities of honey, and to feeding of newly emerged adult males. Males ate honey immediately after emergence. The queen flew 24 hours a day, but at infrequent intervals. She remained away from the nest for longer periods than during the period of sexual larval development and departed permanently soon after the first males emerged.

Peak flight activity for workers was between 1000 and 1700 hours and was not, as yet, a complete 24 hour activity. Flight activity was restricted by food shortage in keeping with reduced nutritional requirements. The population of the nest was also reduced because some foraging workers had died.

On July 24 (Fig. 22), newly emerged third brood queens and some workers were observed in flight at the nest entrance. All collected only nectar. The new queens and workers flew throughout the 24 hour period with no definite peak in activity. The nutritional requirements of the nest were low as the development of the colony was completed, but nectar-gathering was necessary for maintenance of the sexual and worker forms and for preservation of a sufficiently high nest temperature for emergence of the remaining fall queens. Once males had left the nest they did not return.

Weather conditions affected the queen little while she provided for the nest (Fig. 17-18), however she remained within the nest, presumably incubating, during light snow storms on June 17, 1967, and on June 29, 1968. Air temperature at 30 cm above the nest on June 17 was -0.5 C and on June 29 was 4.5 C. Internal nest temperature on June 29 in an artificial nest was 27.0 C and in a natural nest was 19.5 C.

Generally, cloud cover, wind direction, and wind velocity had little influence on frequency of worker flight from the nest entrance. On July 12, 1967, however, mean wind velocity from 0815 to 2230 hours at 15 cm above the ground was 12 mph from the SE (range 7-18 mph), causing approaching workers to land or to be blown to the ground. There, they walked or remained behind the protection of *Salix* and *Saxifraga* clumps before continuing to the nest entrance. Foragers flew into the wind while leaving and returning to the nest when the wind velocity was above 8 mph and did not fly orientation circles. Light showers on July 24 (Fig. 22) reduced flight activity slightly.

The climatic factors affecting circadian periodicity are temperature and sky illumination (Marler and Hamilton 1967), the latter depending mainly on the altitude of the sun. During the part of the season when the workers were flying, the maximum solar altitude varied by three degrees, but within a day the difference between maximum (solar noon) and minimum (solar mid-night) altitude was about 16 degrees. Bumblebee workers did not begin to forage in the morning until the sun was at least 18 degrees above the theoretical horizon. Yet they continued to forage when the altitude of the sun was below 18 degrees for longer periods each day until by July 24 they were flying 24 hours. Thus toward the end of the season the 24 hours of illumination modified any existing periodicity.

Starting about 9-10 C increases in the diel fluctuations of air temperature were correlated to increase in the frequency of flight, and maximum diel air temperature corresponded closely to peak flight activity.

Throughout a season the tendency for food acquisition to shift from pollen-gathering to nectar-gathering and the tendency of foraging hours each day to increase to 24 are behavioral responses to the prevailing weather conditions, to food availability, and to the nutritional requirements of the brood.

The flight activity at the natural nest (Figs. 23-26) was similar to the flight activity at the artificial domicile and any variations (i.e. foraging and brood populations, nutritional requirements) were in the respective nest developments. However, the natural nest queen foraged longer than the artificial domicile queen.

On July 12, 1967, at an artificial nest, the peak of activity was from 1400 to 1800 hours with 57 of 95 workers observed bringing pollen to the nest. The queen and workers did not fly throughout a 24 hour period on that day. Subsequent flight activity observations had ceased by 2200 hours, and by July 19 the flight activity had ceased before 0100 hours.

*Flight in the foraging area.*- Data about duration of flight activity of *B. polaris* workers, males and fall queens, and of *B. hyperboreus* males and fall queens are presented in Table 9. The flight of *B. polaris* workers began in 1967 and 1968, 32 and 18 days respectively after the first *B. polaris* queens had been observed flying and only one day after the first workers had emerged from the brood cocoons. Although flying conditions were favourable until mid-August, no workers were observed to forage after the given dates.

Table 9. Seasonal duration of flight activity of castes and sexes of *B. polaris* and *B. hyperboreus* at Lake Hazen, N.W.T., 1967 and 1968.

Caste or sex	1967	1968
<i>B. polaris</i>		
worker	June 27 - August 10	June 2 - August 5
fall queens	July 21 - August 7	July 23 - August 3
males	July 16 - August 10	July 21 - August 5
<i>B. hyperboreus</i>		
fall queens	July 24 - August 6	July 24 - August 4
males	July 19 - August 6	July 23 - August 6

Generally the flights of bees distant from the entrance was more difficult to record, because on any one day as few as two or three or as many as 66 bees were observed. Thus, the nest entrance flight activity was a more sensitive indicator of field foraging conditions.

Bumblebees flew in close proximity to those habitats where natural nests were located, that is, the distance from the nest that foragers flew was limited.

As low temperatures tend to restrict flight and wind disrupts the warm air produced by insolation of the soil surface (Downes 1955), height of flying above the soil and corresponding air temperature are considered important. The profile of air temperature above the soil surface was measured at a sandy-clay soil site by a thermistor air probe at 1400 hours four times during the summer of 1968 at varying heights. These profiles (Fig. 27) resembled those recorded at Lake Hazen by Powell (1961) and Corbet (1967b) on different days of the season. Abrupt increases occurred within 5 cm of the ground. The pattern was the same for cloudy and windy days (July 15, July 31) and nearly clear calm days (June 30, July 5). On these four days the air temperature was about 7.75 to 10.25 C at the estimated maximum height of flight of queens and workers, and temperature near ground level was about 10.0 C.

Bertram (1935) studied experimentally effects of minimum temperature on *B. polaris* individuals and found that at 9.5 C the bees no longer retained their normal effective activity and at 5 C they became inactive. However, I have observed four queens foraging for nectar from *S. oppositifolia* at - 1.7 C. Gavrilio (1961) reported that bumblebees did not work in temperatures below 4.5 C, nor in frosty fog. At Lake Hazen, bumblebees flew most often at temperatures between 7 and 10 C, although early in the 1967 season, queens flew at temperatures between - 1.7 and 4.4 C.

*Discussion.*- Nutritional requirements and other stimuli originating within the nest affect flight activity. Measurements of honey bee flight at the nest entrance permit a rapid evaluation of the relative effects of intra-nest stimuli (Gary 1967), and this should apply as well to bumblebee colonies. Responses of foraging bees to various combinations of meteorological conditions are as numerous and complex as those to the intra-nest stimuli. One factor predominates at these high latitudes; the daily range of light intensity in clear weather is small, and insects are unable to use the 24 hour light rhythm to synchronize an endogenous cycle (Corbet in Downes 1965). Nonetheless, shifts in flight activity occurred. The queens ceased flying throughout 24 hours when the workers commenced foraging, only to resume again near the end of the season. The workers gradually increased the daily duration of foraging until at the season's end they were flying throughout the 24 hours. But when the colony required the maximum amount of food during development of second and third brood larvae, the queen and workers did not fly throughout the 24 hour period from the nests I observed. However, I believe the workers, shortly after emergence, take their cue for a 24 hour rhythm from the height and position of the sun. Hocking and Sharplin (1964) state that the activity curve for honey bees transported to Lake Hazen was synchronized with Hazen solar time and was unlikely to be due to temperature, since at this latitude the difference between mean maximum and mean minimum temperature during the summer months is less than 5 C. The gradual daily increase in duration of flight activity in response to the 24 hours of light is a significant response to meteorological conditions and may be an adaptation to arctic conditions. Although not statistically tested, other meteorological conditions, such as low air temperature, wind direction and wind velocity, cloud cover, and humidity had less influence on the frequency of flight.

My results indicate that the type of food collected (pollen or nectar) was determined mainly by the brood's nutritional requirements. These depended on the nature and amount of food stores in a colony and especially on the presence and age of larvae in the brood. Collection of food by arctic bumblebees follows the characteristics of lower latitude bees. Number of pollen loads and nectar loads collected at various times of the day by foragers, and the proportion of pollen to nectar loads, shifted gradually from nearly complete pollen-gathering during larval development to nectar-gathering during pupal development. Free (1955a, b) found that the proportion of pollen loads to nectar loads increased during the

day and that the foragers collected pollen only when the carbohydrate stores of their colony had reached a certain minimum level. However, Hasselrot (1960) reports no clear tendency to a forenoon or afternoon preference in pollen-gathering on separate days. Variation of the proportions may indicate the stage of colony development.

Bumblebees develop considerable heat from the activity of the flight muscles (Newport 1837, Hasselrot 1960) and the long shaggy hair of members of *Alpinobombus* enables them to keep active in low temperatures (Sladen 1919, Friese 1923a). During flight, size of the insect and density of the coat are more important for insulation than length of the hair, though they seem to be of negligible value when at rest (Church 1960).

Arctic bumblebees show pronounced melanism and members of the species *B. (Alpinobombus) balteatus*, *B. (Pyrobombus) melanopygus* Nyl., *B. (P.) mixtus* Cress., *B. (P.) sitkensis* Nyl., *B. (P.) sylvicola* Kby. of the Boreal Cordilleran transition zone of Alberta (Hobbs 1967b) also have a tendency to melanism. This dark coloration, generally rare in the North American bumblebee fauna (Sladen 1919), increases absorption of solar radiation. The ability to be warmed by solar radiation is greater in workers because of their reduced size and resulting greater ratio of area to volume (Downes 1926). Thus, large size, long, dense hair and dark coloration are factors which allow bumblebees to be warmed by solar radiation. The relatively low height of flight suggests that bees obtain warmth from radiation reflected from the soil.

### Nest temperature

Bumblebees, like some other social Hymenoptera, are capable of partly regulating their body temperatures independently of external air temperatures, and can, singly or collectively, regulate nest temperature. A study of temperature relations of arctic bumblebee colonies at various stages of development was made to estimate brood temperature. Effect of arctic climatic conditions on brood temperature is discussed and a comparison is made between temperatures of the artificial domicile and a natural nest.

Data on the meteorological conditions and diel periodicities affecting brood temperatures were presented in the flight activity section. Previous investigations of temperatures in bumblebee nests were by Himmer (1933), Nielsen (1938), Hasselrot (1960), Wójtowski (1963a, b), Newport (1837), Plath (1934), Cumbér (1949), and Brian (1952). Fye and Medler (1954) gathered temperature data from bumblebee nests in domiciles of varying construction and insulation. Hobbs, Nummi and Virostek (1962) investigated behavioral mechanisms of temperature control in above-ground artificial domiciles. Newport (1837), Sladen (1912), Free and Butler (1959), and Hasselrot (1960) reported heat generation and temperature regulation by the body temperature in nests.

*Material and methods.*- Measurements of brood temperature and flight activity investigations at the nest entrance were made at the same time. Prior to July 6, temperatures were taken with surface thermistor probes placed under, and (Fig. 10) as near as possible to, the center of the first brood larvae. After July 6, brood temperatures within each nest were recorded each hour with a dial thermometer. Temperatures of the brood were measured at one to two minute intervals while the queen was foraging, to determine fluctuations and dependence of the first brood on the queen for incubation temperature.

*Results.*- Temperature curves obtained for the artificial domicile nest (Figs. 17-22) and for the natural nest (Figs. 23-26), reflect the development of the colonies.

While only the queen was incubating the brood (Figs. 17-18), variations in nest temperature were related to her absences and were numerous during first brood larval development (Fig. 17). On 20 occasions (Fig. 17) and at different air temperatures, the nest temperature decreased an average of 0.22 C per minute while she foraged. The average rate of increase on her return was 0.43 C per minute, and on the average 14.5 minutes elapsed before the original temperature was attained. Thus the temperature of the brood increased about twice as fast as it decreased while the queen was away, presumably because of brood metabolism. On seven occasions while the queen foraged during first brood pupal development nest temperature decreased at an average rate of 0.30 C per minute and increased 0.27 C per minute on the average when she returned. On average, 22 minutes elapsed before the former nest temperature was attained. The different rates probably result from the lower resting metabolism of pupae.

Queens remained in the nest a longer time after greater temperature drops (e.g. Fig 17, from 1225 to 1545 and Fig. 18, from 1320 to 1625). When these lengthy compensations occurred the nest temperature was as low as or lower than 21 C which may be the minimum temperature for normal first brood larval and pupal development. During this stage maximum nest temperatures are related to the higher air temperatures, but not to the maximum diel temperature, which occurred between 1300 and 1600 hours (Corbet 1966, 1967b). The differences between nest temperature and air temperature were 19 to 22 C. The minimum nest temperatures while the queen was in the nest are related to the minimum air temperatures with differences of 20 to 24 C. Hasselrot (1960) termed this period of instability and variation the "period of upbuilding." During the "period of equilibrium" (Hasselrot, 1960), the nest temperature was 18 to 24 C higher than the outside temperature. The variations for July 6 (Fig. 19), were between 30 and 35 C, and for July 12 (Fig. 20) were between 27 and 33 C. The tendency for the nest temperature to vary in accordance with the variations in the external temperature was not noted in the artificial domicile at this stage of brood development.

During the "period of decline" (Hasselrot 1960), (Figs. 21, 22) temperatures gradually decreased and variations for July 18 (Fig. 21), were between 19 and 28 C with the maximum nest temperature 5 to 7 C warmer than the maximum air temperature and the minimum nest temperature 13 C warmer than the minimum air temperature. Nest temperature variations for July 24 (Fig. 22), were between 10 and 20 C with 5 to 8 C difference from the air temperature.

External air temperature fluctuations influenced the natural nest temperature (Figs. 23-26) more than the temperature of the artificial domicile nest. In addition to those climatic conditions resulting directly from solar radiation, other climatic factors, such as light snow and rain, had more influence on the natural nest than on the artificial domicile nest. Data indicating the insulating effects of the styrofoam are shown in Fig. 18.

*Discussion.*- The three periods of nest temperature sequence (Hasselrot 1960) were clearly discernible in the artificial domicile nest. The period of upbuilding was characterized by temperature variations caused by absence of the foraging queen. Because the volume of the nest had increased during development of first brood pupae and second brood eggs, the rate of rewarming was slower and time required by the queen to rewarm the nest was longer than during first brood larval development. The period of equilibrium was characterized by stable nest temperatures not in accordance with the outside temperatures. As this was the period of maximum nest population, maximum flight activity, and maximum nutritional requirements, maximum continuous nest temperature was expected. These higher temperatures provided optimum conditions for the work and growth of the colony, and are desirable factors for queen production (Cumber 1949). The period of decline was characterized

by gradually increasing variations in nest temperature which closely agreed with the outside temperature. Decline in the nest temperature is probably connected to the lack of honey in the colonies, caused by the sexual forms using up the supply, and by the disintegration of the colony (Hasselrot 1960).

Results of 24-hour temperature readings in the artificial domicile nest indicated that maximum and minimum nest temperatures were close to the maximum and minimum diel air temperatures. Worker foraging movement in or out of the nest appeared not to influence the nest temperature. Because of the few lengthy observations, the temperature phenology in the natural nest could not be followed, but I believe that it would be the same as for the artificial nest.

The natural nest temperature was more dependent on the external air temperature and the brood was subjected to more severe environmental factors than the artificial domicile nest which had the protection of the styrofoam lid. Even with these nest temperature differences, the time did not vary for each brood to complete development. Generally, more eggs, larvae, pupae, emerging adults of the second and third broods, and food were found in the artificial domicile nests than in the natural nests.

The danger of overheating the nest through excessive insulation is, according to Himmer (1933), very small. Workers of *B. polaris* increased the air flow and regulated temperature of the domicile nest by fanning with their wings at the tunnel entrances. Hasselrot (1960) found that workers began to vibrate their wings at a nest temperature of about 33 C and 13 C in the surrounding air. Workers were not observed to fan any of the natural nests; small ventilation holes in the wax-pollen and moss canopies were present.

Nest temperature curves obtained for these arctic bumblebees were similar to the temperature curves obtained by Himmer (1933), Nielsen (1938), Hasselrot (1960), and Wójtowski (1963a, b) for members of other species of bumblebees.

### Food preference

Competition among insects for available nectar and competition among plants for services of pollinating insects have been discussed by several authors (Knuth 1906-1909; Clements and Long 1923; Grant 1950; Brian 1954; Hocking 1968). The purposes of this section are to establish adaptations and relationships of arctic bumblebees to arctic flowers. The phenology and constancy of visitation and usage within the nest were investigated.

The literature on flower constancy for all Apidae was reviewed by Grant (1950) and Brian (1954). Høeg (1924, 1929) reported on degree of constancy to pollen of various species exhibited by bumblebees from Novaya Zemlya and Ellesmere Island. Cockerell and M'Nary (1902) suggest that arctic bumblebees visit a great variety of plants because they have few competitors, but McAlpine (1965b) and Hocking (1968) disagree. In the arctic regions, pollination biology of plants, and pollen on bumblebees have been investigated by McLachlan (1879), Ekstam (1894, 1897, 1899), Jacobson (1898), in Fries (1902, 1904, 1908, 1923a,b), Sparre-Schneider (1906), Johansen and Nielsen (1910), Frison (1919), Sladen (1919), Johansen (1921), Høeg (1924, 1929), Richards (1931), Longstaff (1932), Brinck and Wingstrand (1951), Holmen (1957), Bruggeman (1958), Freuchen and Salomonsen (1958), Savile (1959), Gavriliok (1961), Løken (1961), Swales (1966), Milliron and Oliver (1966), Mosquin and Martin (1967) and Hocking (1968).

Angiosperm pollen is the main source of protein (Auclair and Jamieson 1948, Weaver and Kuiken 1951), fat (Hügel 1962), vitamins (Schwarz and Kock 1954, Bukatsch and Wildner 1956) and minerals (Lubliner-Mianowska 1956) which a bumblebee colony needs to maintain itself.

Sugars (carbohydrates) present in the nectar of flowers of various species have been investigated by Wykes (1952a). She found that mono- and oligosaccharides (fructose, sucrose, and glucose) were in nectar of nearly every species tested. Traces of maltose, melibiose, and raffinose were in nectar from flowers of some species. Studies by Park (1930), Hocking (1953, 1968), Wykes (1950, 1951, 1952a, b, c), Manning (1956), and Shuel (1967) show that volume and total sugar concentration of nectar secreted by individual flowers varied widely, both intra- and inter-specifically. Thawley (1969) reviewed the composition and properties of honey.

Sladen (1912), Plath (1934), Free and Butler (1959), and Knee and Medler (1965) described two types of honey found in bumblebee nests: "thin" and "thick." Sladen (1912) described thin honey as that found in wax honey pots constructed by the established queen and later by workers. He believed thin honey was freshly gathered and consumed each day. Thick honey was recorded from old empty cocoons and was considered to be stored for times of scarcity.

The annual duration of growth and seasonal succession of flowering of plant species (Sørensen 1954, Hocking 1968), is significant to the survival of bumblebees especially during August and September when flowers become scarce. Sørensen (1941) in northeastern Greenland distinguished five phenological seasons, which followed each other in rapid succession and which Powell recognized as being shorter in duration at Lake Hazen. Powell (1961) compared the phenology of Lake Hazen, with Alert, Northwest Territories, and Es-kimona, Greenland. Hocking (1968) indicated seasonal peaks for four common species of plants during three years.

*Materials and methods.*-Observations of bumblebee foragers on flowers at Lake Hazen include records of flower species, constancy, and possible flower pollinating mechanisms.

To support visual observations and to indicate which flowers were used and why, 406 samples of pollen and nectar were taken from 15 nests in 1967 and 134 samples from 22 nests in 1968. Samples were taken throughout the summer during each brood observation. The samples consisted of fresh moist pollen from under the larvae and pupae, from the corbiculae of incoming or field foragers, from wax from honey pots, from brood and canopy, from nectar from the honey pots and brood, and from fresh bee feces.

Pollen and nectar from the nest and pollen from corbicular loads were mounted in glycerine jelly tinted with basic fuchsin for identification by comparison with photographs of samples in a reference collection of flowers in the research area. Pollen identifications were based on sculpture and form only.

*Flower preferences.*- The phenology for 1958 from Powell (1961) and for 1962 from Savile (1964) and from my two summers' work is presented in Appendix II, of Richards (1970). A comparison of dates for these four seasons at Lake Hazen shows tremendous variation but indicates the sequence in which "bumblebee flowers" are visited and used.

Data about phenology of bumblebee flowers, date of first occurrence of *B. polaris* queens, workers, and males and the period of utilization for 1967 and 1968 are presented in Fig. 28, which was constructed from nest samples of pollen and nectar and from dates of observations. Table 10 summarizes data from observations of the flower species which individuals of *B. polaris* and *B. hyperboreus* visited.

Table 10. Number of observations of *B. polaris* and *B. hyperboreus* individuals at flowers of various species at Lake Hazen, N.W.T., 1967 and 1968.

	<i>Bombus polaris</i>			<i>Bombus hyperboreus</i>		
	♀ old	♀ new	♂ new	♀ old	♂ new	♀ new
1967 <i>Saxifraga oppositifolia</i>	49	1		2		
<i>Salix arctica</i> (♀ ♂)	20	1		1		
<i>Dryas integrifolia</i>	4	44	3	1	1	
<i>Cassiope tetragona</i>		10				
<i>Papaver radicatum</i>		2	1			
<i>Pedicularis arctica</i>	30	9		5		
<i>Pedicularis capitata</i>	5	5		4		
<i>Melandrium affine</i>		1				
<i>Stellaria longipes</i>		1	6			1
<i>Silene acaulis</i>				1		
<i>Arnica alpina</i>		1				
<i>Polygonum viviparum</i>			1			
Total	108	75	11	14	2	
1968 <i>Saxifraga oppositifolia</i>	23	3		4		
<i>Salix arctica</i> (♀ ♂)	36	1	2	1		
<i>Dryas integrifolia</i>	4	16		5		
<i>Cassiope tetragona</i>		13	3			
<i>Stellaria longipes</i>		10	7			
<i>Pedicularis arctica</i>	23	15		3		
<i>Pedicularis capitata</i>	19	19		2		
<i>Saxifraga tricuspidata</i>		8	2			
<i>Polygonum viviparum</i>			3			
<i>Arnica alpina</i>		1				
<i>Silene acaulis</i>				1		
<i>Epilobium latifolium</i>		8	18			
Total	105	94	35	16		

The main flowers at Lake Hazen which bumblebees visited for food are members of the species *Saxifraga oppositifolia*, *Cassiope tetragona*, *Pedicularis arctica*, *Pedicularis hirsuta*, *Salix arctica* (male and female), *Dryas integrifolia*, *Pedicularis capitata* and *Stellaria longipes*. Flowers of the species *Silene acaulis*, *Arnica alpina*, *Polygonum viviparum*, *Saxifraga tricuspidata* and *Epilobium latifolium* are occasionally visited near the end of a season when the more popular flowers are scarce. A few pollen grains of *Cerastium* sp. were collected late in the season from three honey pots of two nests, which indicates that these flowers were sparsely used for nectar. Flowers visited at the end of the season were those late in growing as indicated in the dates of flower phenology (Richards 1970). Thus the rapid active season affected flower phenology and flower visitation. At the end of the season, only nectar was collected from the flowers.

The composition of 70 pollen pellets was as follows: 35 consisted of pollen from one plant species; 27 of pollen from two plant species; 6 of pollen from three plant species and 2



of pollen from four plant species. I saw 459 bumblebees visit flowers during 1967 and 1968. Of these, 13 visited flowers of two species, and three visited flowers of three species. The rest yielded no evidence of having visited flowers of more than a single species. Foragers visited a wide range of flowers throughout the season, but at any one time they visited members of only a few species. For example, before workers emerged, queens visited only *S. oppositifolia* and *S. arctica* flowers, but when these flowers were scarce the foragers visited others.

In this study 254 samples of honey from 12 nests in 1967 were analyzed for sugar concentration. At Lake Hazen thick honey first appeared in nests when workers began to forage. The number of honey pots increased as the second and third brood larvae were being fed, but the numbers in use declined when the first males emerged. Most of the incoming nectar was placed in the honey pots from which the sexual adults fed. From queen acceptance of a nesting site until final brood decay, in one nest, the concentrations of total sugars tested, (Fig. 29) showed a gradual increase from thin to thick honey. Concentrations from other nests indicated this same trend. As expected, the mean honey concentrations varied from nest to nest and from honey pot to honey pot within the same nest on different days. Possible reasons for the difference in sugar concentration are water evaporation (Plath 1934) and quantitatively selective feeding (Free 1955b).

Total sugar concentrations of thin and thick honey are almost always higher, probably because of water evaporation, than are total sugar concentrations of nectar (Hocking 1953, 1968).

Adults of *B. polaris* and *B. hyperboreus* have been recorded to visit flowers of 43 species of plants distributed among 36 genera and 18 families. See Richards (1970, Appendix III) for a list of species names of plants visited.

*Discussion.*- The dependence of these bumblebees on flowers for nutrition is perhaps greater than the dependence of the flowers on bumblebees for pollination. Bees were recorded foraging for pollen and/or nectar from members of 15 plant species at Lake Hazen and from members of 36 genera in this and other arctic localities. This alone indicates that 'bees in the arctic tend to become less restricted in their choice of flowers' (Richards 1931) and that they 'specialize in being unspecialized' (Savile, pers. comm. 1969). The 50% constancy (35 out of 70) in flower visitation of these arctic bumblebees is in close agreement with the total figure given by Brian (1954) for various other members of *Bombus*, but is much higher than the figures given by Høeg (1924, 1929) although he analyzed the pollen from other parts of the body besides the corbiculae.

Almost all plants beyond the tree-line are self-fertile, and several are apomictic - necessary safeguards against frequent seasons when insect activity is severely restricted during the period of bloom (Savile, pers. comm. 1969). But, McAlpine (1965a) Hocking (1968) and Kevan (1970) have stated that a number of anthophilous Diptera are important arctic pollinators, a fact which indicates that some cross-pollination occurs in many flowering species. Hocking (1968) believes that flowers at Lake Hazen compete for pollination rather than that pollinators compete for nectar. Arctic bumblebees are pollinators only of those flowers from which they forage extensively. Other less important bumblebee-visited flowers are doubtful benefactors; however, there are exceptions such as *S. longipes* and *E. latifolium*.

As the presence and abundance of the arctic bumblebee-visited plant species vary within the Canadian Arctic archipelago and generally within the whole arctic, the usage by the bumblebees also varies. For example, *Silene acaulis* which several authors reported to be abundant and visited by bumblebees on Novaya Zemlya, was rare and rarely visited at Lake Hazen. Other examples are in the Cruciferae, Ericaceae, and especially Leguminosae. The

many possible ecological niches as yet unoccupied (McAlpine 1964, 1965a) are another reason for the variable usage by bumblebees.

## NEST PARASITISM AMONG HIGH ARCTIC BUMBLEBEES

Bumblebees of the genus *Psithyrus* are known to parasitize nests of various species of *Bombus*, (Free and Butler, 1959) and intraspecific and interspecific nest parasitism has been recorded for *Bombus* (Hobbs, 1965a,b and 1967b). Yarrow (1970) suggests that *Bombus inexpectus* behaves like a workerless obligate parasite, similar to *Psithyrus*, but biological data are lacking. Reported here are observations establishing intra-specific nest parasitism in *B. polaris* and interspecific nest parasitism of *B. hyperboreus* on *B. polaris*. These findings are discussed in terms of the evidence they provide concerning origin and evolution of nest parasitism among bumblebees.

### Intraspecific nest parasitism

In 13 natural nests a second *B. polaris* queen was found after the original queen had initiated and established a first brood. In each nest one of the two queens was dead. The nail polish markings on them established that in five instances the foundress was the victor of a previous fight; in three instances the intruder was victor; and in five, history of the victor was unknown. The intruding queens were observed nest-seeking as late as early emergence of first brood adults. These intruders did not initiate broods of their own but assisted the foraging workers. No disturbances, such as removal of larvae or destruction of egg cells, were noted in the nests. Milliron and Oliver (1966) reported one instance of intraspecific nest parasitism in *B. polaris*.

### Nest parasitism by *Bombus hyperboreus*.

Interspecific associations of *B. polaris* and *B. hyperboreus* indicate a host-parasite relationship. Unlike other *Bombus* queens, those of *B. hyperboreus* do not establish nests of their own and do not produce workers over most of the range of the species. A solitary life with production of few or no workers was indicated for the sexual stages of *B. hyperboreus*, *B. balteatus* and *B. polaris* (Jacobson 1898; Friese, 1902, 1904, 1908, 1923a,b; Friese and Wagner, 1912). A parasitic mode of life was not suggested. Richards (1931) reported a worker to female ratio of 0.2, and Milliron and Oliver (1966) reported examining about a dozen museum specimens of *B. hyperboreus* workers, mostly from Scandinavian localities - probably the same material as was examined by Richards.

Other authors (Strand 1905; Richards 1931; Henriksen 1937, 1939; Brinck and Wingstrand 1951; Bruggeman 1958; Milliron and Oliver 1966 and I) reported only *B. hyperboreus* queens and males from various localities. Milliron and Oliver (1966) made preliminary observations at Lake Hazen on usurpation by *B. hyperboreus* females of nests of *B. polaris*. I made observations to determine if females of *B. hyperboreus* were parasitic on colonies of *B. polaris*.

*Observations.*- Individuals of *B. hyperboreus* emerged later in the season and were not as abundant as were individuals of *B. polaris*. Nest-seeking behavior was similar to that of *B. polaris*, except that *B. hyperboreus* queens did not initiate nests of their own.

Queen *B. hyperboreus* searched primarily along cracks in clay and in lemming holes for nesting sites of *B. polaris*, flying usually less than 25 cm above the ground. Most *B. hyperboreus* queens were seen previous to or after *B. polaris* workers of the first brood had emerged.

The following is a description of the behavior of a *B. hyperboreus* queen from the time of her first discovery of a *B. polaris* natural nest until she remained within the nest 58 minutes. The observation was made June 28, 1967, from 0030 to 0330 hours on a clear, calm, 9.0 C night in a marsh sedge meadow (M8, Fig. 6):

"The *B. hyperboreus* queen first approached the nest flying less than 25 cm high. She flew three or four orientation circles before landing and entering the 210° facing entrance. After defensive behavior (ie. rapid movement of the wings) by resident workers she retreated from the nest to a nearby moss clump where she groomed herself. Grooming consisted of rubbing the fore-and mid-legs over the head and thorax and hind-legs over the sides of the abdomen. She was repelled from the nest 13 times by the workers and queen before she gained acceptance. Twice the workers blocked the entrance to the intruding queen by lying upside down with the sting protruding and once two workers followed her about 60-75 cm from the nest. The *B. hyperboreus* queen, after being repelled from the nest, either groomed or visited flowers which were nearby. The grooming procedure was repeated many times. The *B. hyperboreus* queen did not orient back to the nest but flew directly."

I found in the nest at 0830 hours the same morning a *B. polaris* queen dead beside the honey pot and, near the nest entrance, eight *B. polaris* workers (either collecting pollen and nectar or warming the brood) eight first brood pupae near emergence and an active *B. hyperboreus* queen. During the examination the queen remained (except when I moved her) on top of a rough new egg cell built on the side of the incubation groove and containing seven horizontally laid eggs. As the queen appeared to be protecting this egg cell, I presumed she had laid the eggs. An arctic fox destroyed this nest two days later.

In five nests which had living *B. hyperboreus* queens, the host *B. polaris* queen was dead. More than one *B. hyperboreus* queen was collected in one nest with the latest nest-seeking queen alive. Seventeen dead *B. hyperboreus* queens were found in *B. polaris* nests as victims of an arctic fox. Milliron and Oliver (1966) reported two composite nests of *B. polaris* and *B. hyperboreus* sexuals, as adults or brood. They hypothesized that the establishing *B. polaris* queen was driven off by the usurping *B. hyperboreus* queen.

## ADAPTATION OF BUMBLEBEES TO THE ARCTIC ENVIRONMENT

Characteristics of *Bombus polaris* may be regarded as a series of adaptations permitting members of this species to live under conditions imposed by the high arctic environment. Briefly stated, these conditions are: low temperature, small heat budget, reduced growing season with continuous or almost continuous daylight, and high water table with permafrost near the ground surface.

Normal nesting sites for bumblebees are abandoned nests of rodents, shrews or birds, either on or below the surface of the ground. In temperate areas, such sites provide warm shelter. In the high arctic, however, rodent nests (specifically those of lemmings) are unsuitable for bumblebees because they are cold and frequently wet. Although queens investigate these nests, they rarely use them, but instead nest in marsh and sedge meadows, which provide warm and dry sites, with an abundance of suitable nesting materials. The selection of these sites is an adaptation for life in the high arctic environment.

The relatively short period of growth available each year to arctic bumblebees is selective for rapid colony development. This could be achieved by increased rate of growth (ie., individual development), or by decreased time required to complete processes associated with development of the colony. Rate of development of individuals of *B. polaris* is the same as in more southern bumblebees, so the first alternative strategy was not adopted. Length of the annual life cycle was reduced by processes employing the second alternative. This re-

duction was achieved by production of only a single brood of workers prior to production of sexual forms; by a large first brood, providing proportionately more workers; by reduction in time required by the queen to provision first brood larvae and increase effectiveness of incubation; by laying all eggs in a single cell and feeding the larvae collectively; by a high rate of food provisioning, related to the more or less continuous foraging activities of workers in continuous daylight, and by acceptance of a wide variety of flowers by foragers. Structural and functional adaptations for flight at low temperature are the following: large size, long dense hair and dark coloration. These are factors which allow the bumblebees to be warmed by solar radiation. The relatively low height of flight of workers suggests that they attain additional warmth from the radiation reflected from the soil; at the same time they encounter lower wind speeds.

Members of *B. hyperboreus* exhibit structural and general behavioral features similar to those of *B. polaris*, so both species are similarly adapted for life in the arctic environment. Parasitic behavior patterns are special adaptations for life in an adaptive zone not restricted to one set of physical and biotic factors, and in this sense nest parasitism cannot be regarded as adaptive to the arctic. However, a parasitic mode of existence further shortens the annual life cycle of a species, and in this sense, it is adaptive in the far north. The intriguing question frequently asked: "Why are bumblebees found in the high arctic" can (perhaps) now be answered. Bumblebees and their host plants, being mutually dependant, must have dispersed northwards at the same time and during this process *B. polaris* and *B. hypoboreus* became adapted to environmental conditions that differed from those further south. These adaptations do not appear to involve large changes in physiology, morphology or behavior when the variation in the factors among all bumblebees is considered.

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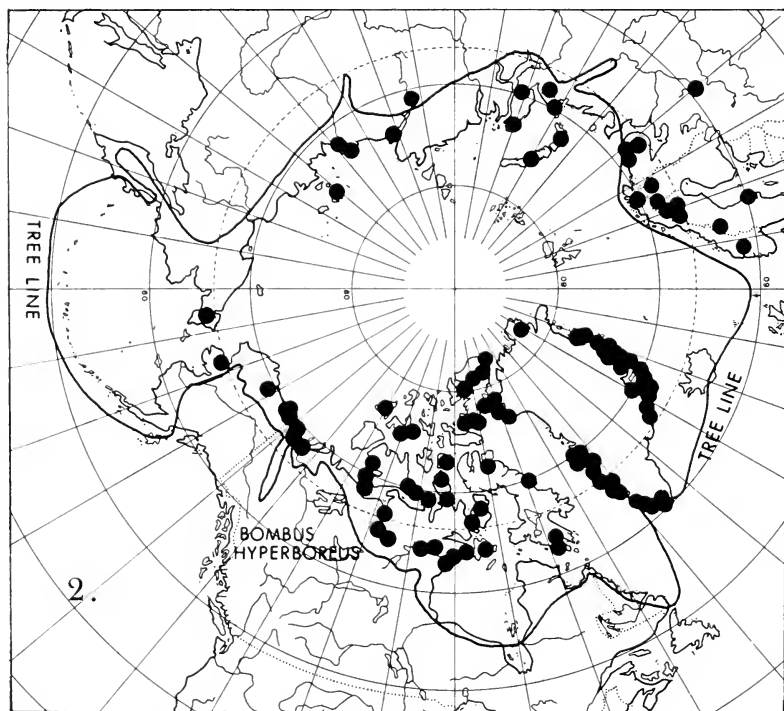
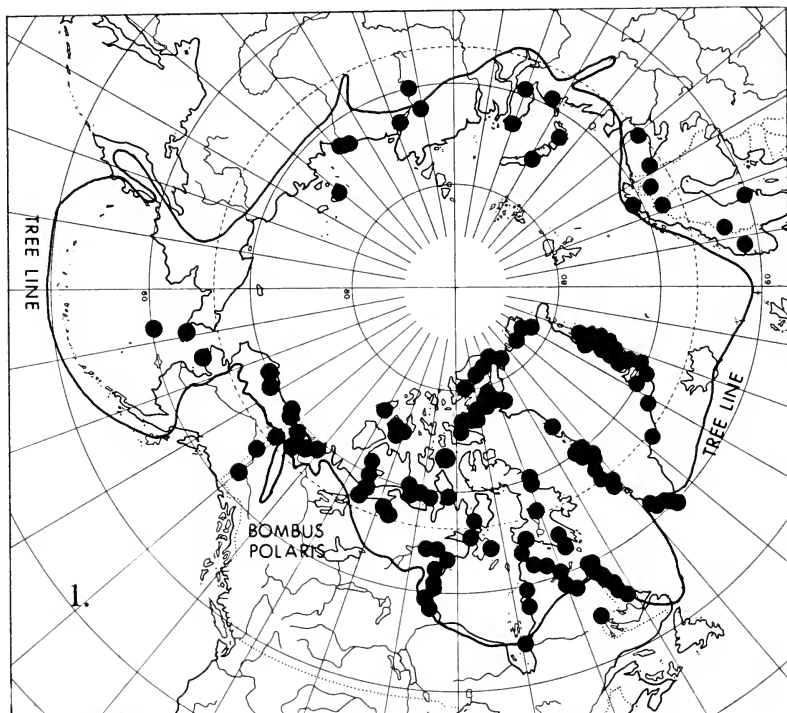
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Figs. 1-2. Geographical distribution maps. 1. *Bombus (Alpinobombus) polaris* Curtis. 2. *Bombus (Alpinobombus) hyperboreus* Schönherr.

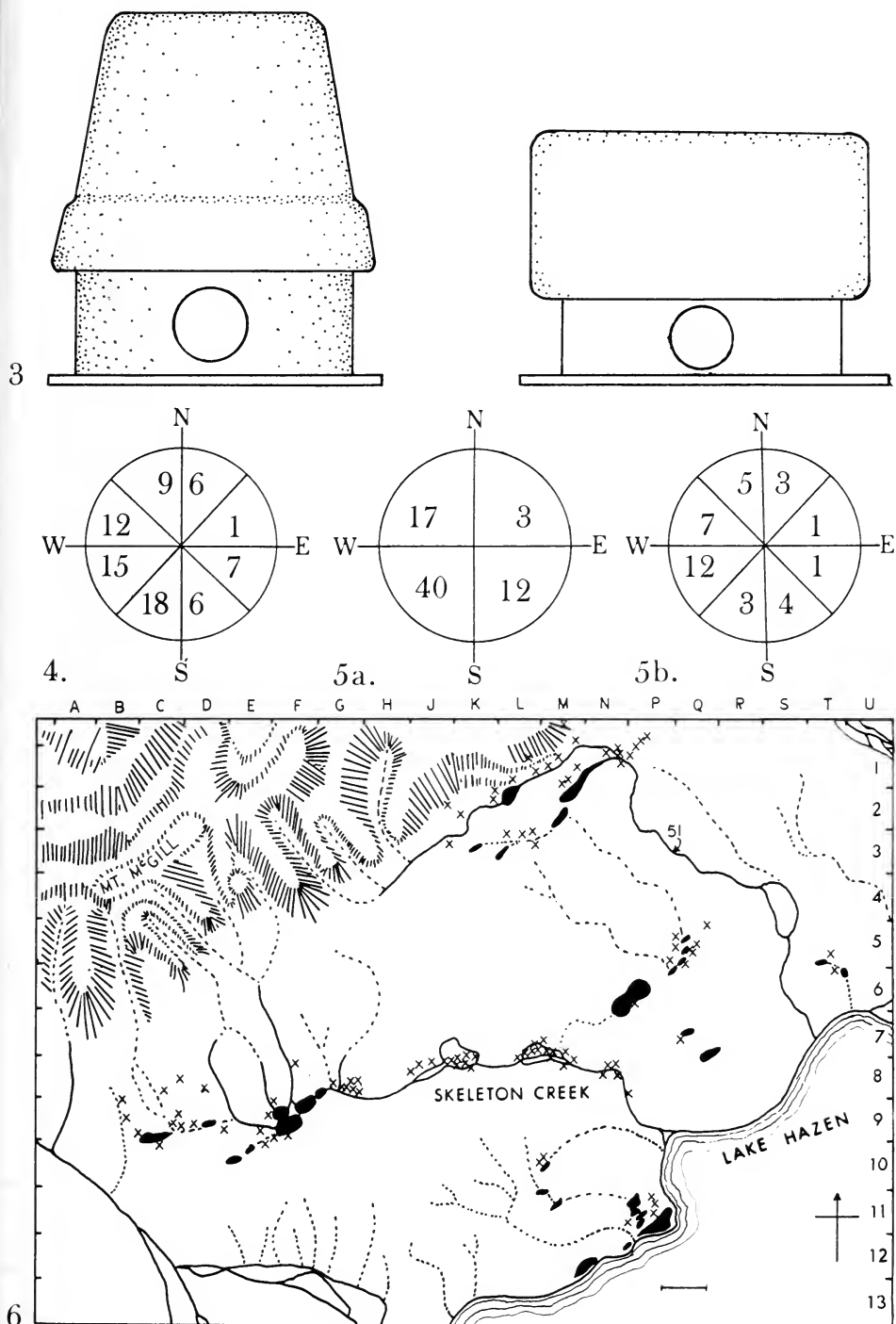


Fig. 3. Two basic types of small, light weight artificial domiciles, one-half size. Fig. 4. Numbers of *B. polaris* queens investigating different lemming holes by points of the compass at Lake Hazen, N.W.T., 1967 and 1968. Fig. 5. Generalized hummock or moss mound, numbers of nests of *B. polaris*: a, by quarter hummock or moss mound; b, number of nest exits by compass point. Fig. 6. Distribution of *B. polaris* natural nests (marked X) in the Lake Hazen study area. Map modified from Savile (1964). Accompanying scale divisions equal 1000 feet.

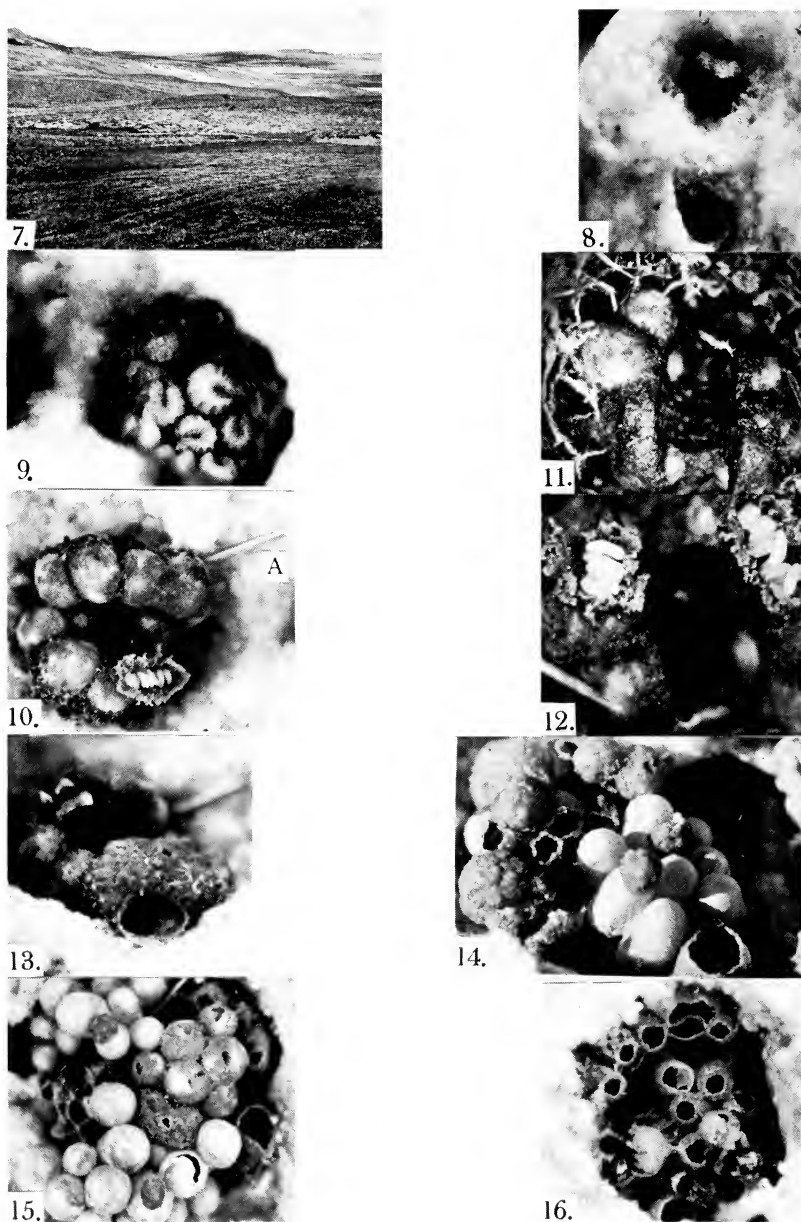
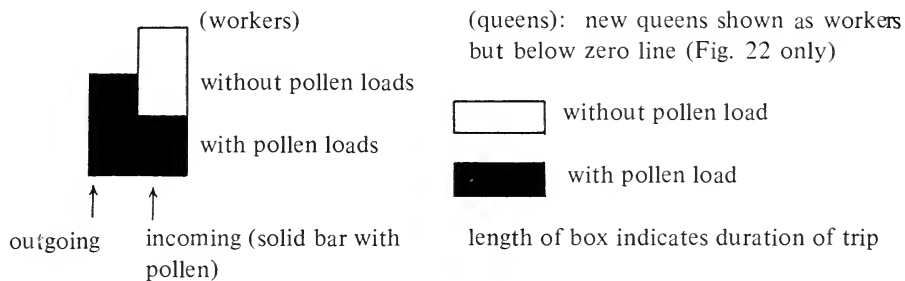


Fig. 7. Typical marsh and sedge meadow (K8) in which *B. polaris* queens established natural nests. Stakes indicate location of nests. Fig. 8. First brood cell of *B. polaris* with honey pot and brood with wax-pollen canopy intact. Fig. 9. Exposed first brood larvae showing curled position. Fig. 10. Second brood (male) eggs on top of first brood cocoons; the eggs have been exposed to show their horizontal orientation. A—thermistor probe. Fig. 11. Second brood egg cells on the outside tops of the cocoons that formed the sides of the incubation groove covered first. Fig. 12. Same brood cells as Fig. 11. with the two groups of eggs exposed showing the front half of the incubation groove. Fig. 13. Close-up of pollen receptacle on the side and beneath the second brood (male) larvae. Fig. 14. Egg cells of the third brood (queen) on top of the newly spun male cocoons. The large pollen receptacle is beside and beneath the male cocoons. Fig. 15. Brood exposed showing male cocoons (center top and bottom), exposed last-instar queen larvae (right), egg cells on top of male cocoons, and pollen receptacle (extreme right). Fig. 16. All but one queen egg cell (left) emerged, and many honey pots (top center) nearly empty. A varying time lag is apparent in nest temperature changes resulting from external events. This is attributable to varying low conductivity of nest material plus thermometer response time.

Figs. 17-26. Flight activity, weather, and nest temperature of *B. polaris*, 1968, at Lake Hazen, N.W.T.

Explanation of symbols:

Flight activity:



Temperature, air  $\times$ — $\times$ , in artificial domicile nest  $\bullet$ — $\bullet$ — $\bullet$ ,

Temperature in nest; continuous —, 30 minute mean  $\bullet$ — $\bullet$ .

Angular elevation of sun from Corbet (1966):  $\Delta$

Wind direction  $\uparrow$ ,  $\leftarrow$  E,  $\downarrow$ ,  $\rightarrow$  W, variable  $\times$ , velocity in mph  $\circ$ —, S N

Cloud cover 0/8  $\bigcirc$ , 2/8  $\bigcirc$  (1/4 shaded), 4/8  $\bigcirc$  (1/2 shaded), 6/8  $\bigcirc$  (3/4 shaded), 8/8  $\bullet$ , rain  $\bullet$  (Fig. 22 only)

Time: eastern standard, 00=24=midnight.



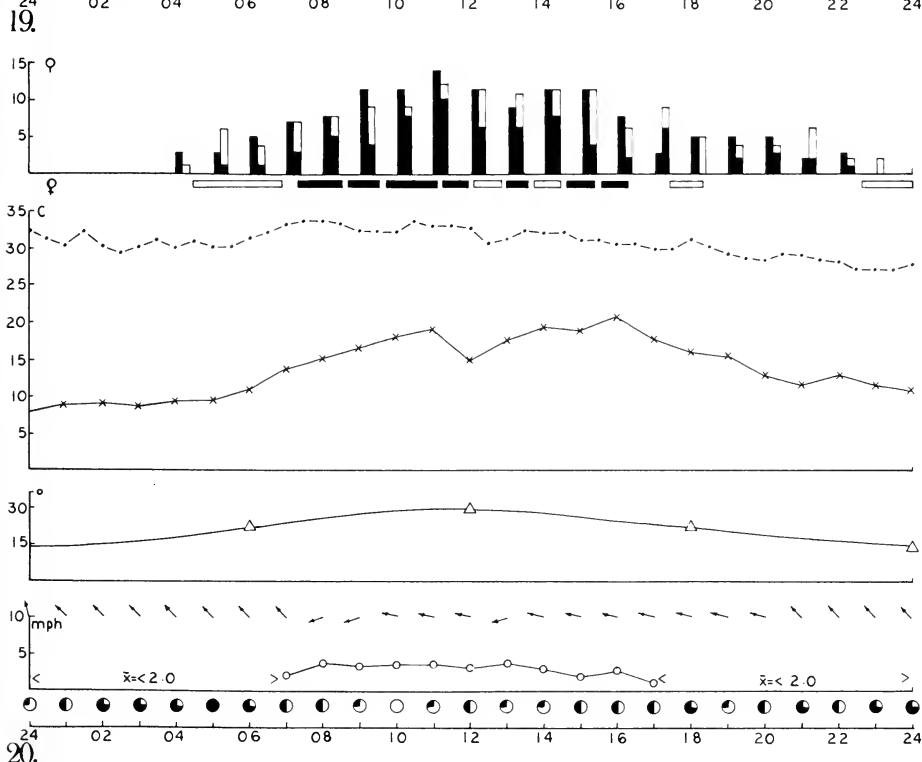
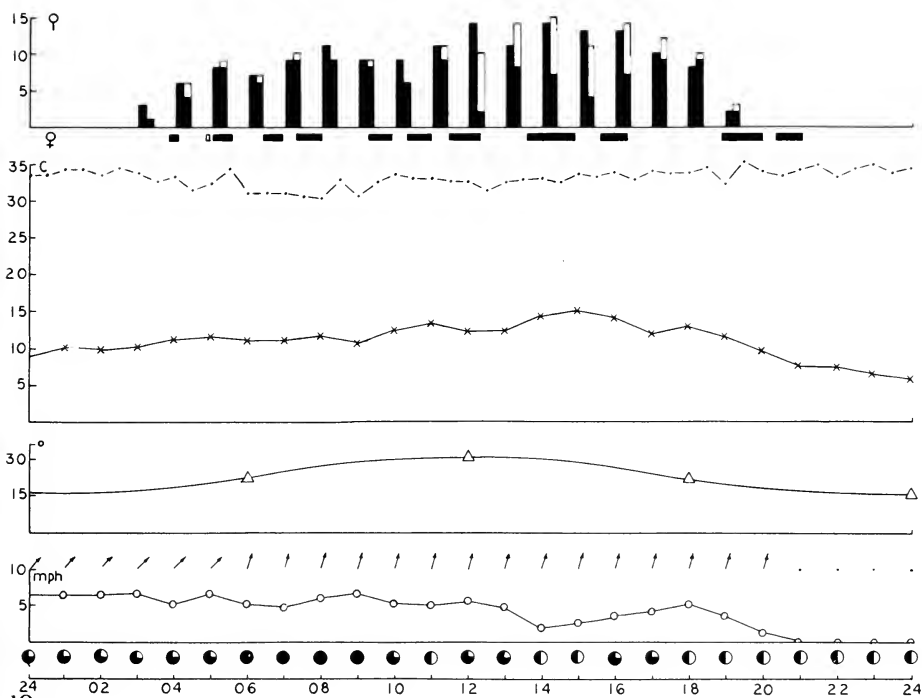


Fig. 19. July 6, 1968; one queen, 16 workers, second brood of 14 late-instar larvae, 10 early pupae, third brood of 10 eggs.  
 Fig. 20. July 12, 1968; one queen, 14 workers, second brood of 24 late-pupae, third brood 6 eggs, 10 mid-larvae. For explanation of symbols see page 149

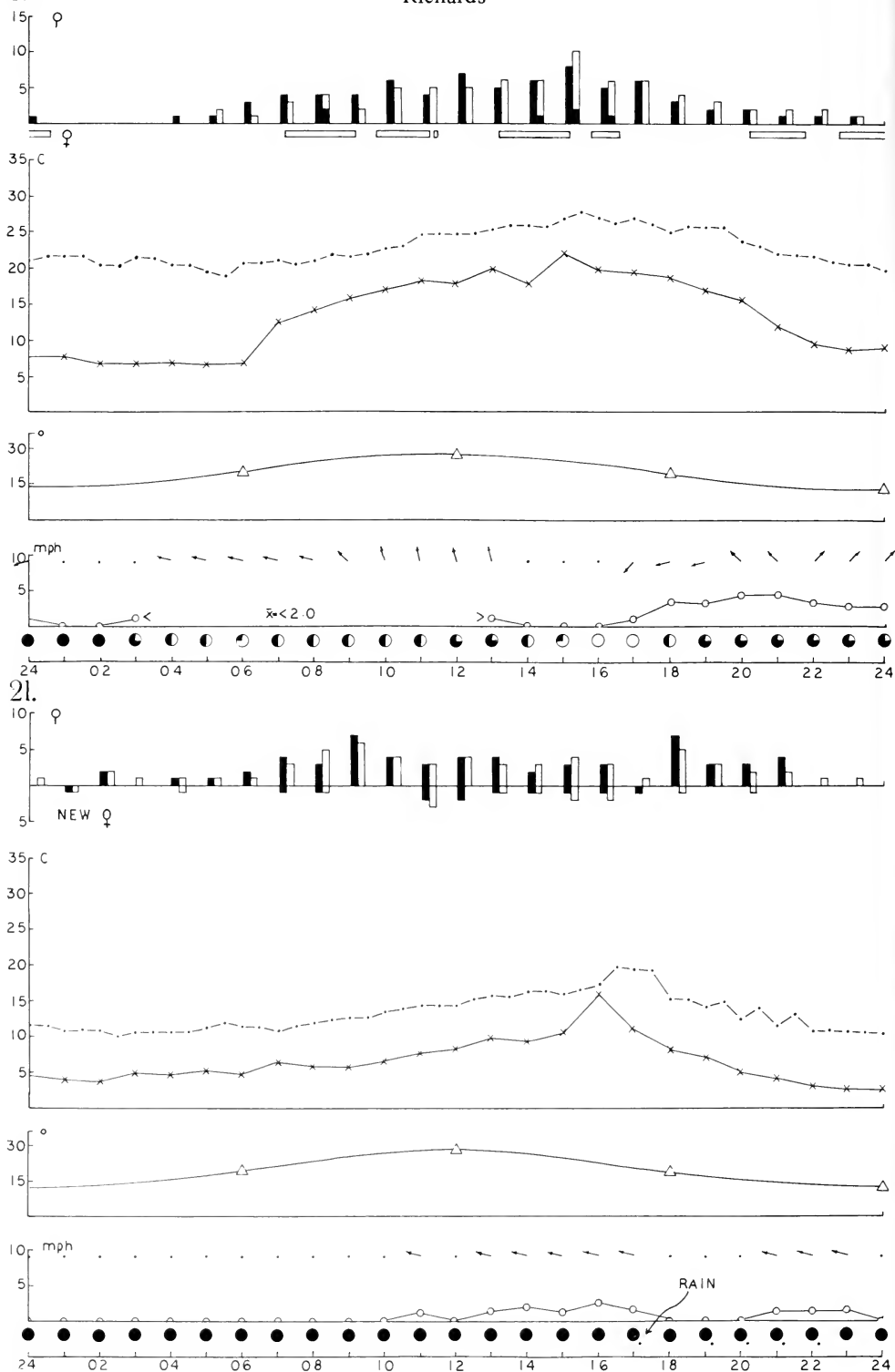


Fig. 21. July 18, 1968; one queen, 10 workers, 3 males, second brood 21 late-pupa, third brood 6 eggs, 10 pupae. Fig. 22. July 24, 1968; 9 workers, 5 fall queens, 2 males, third brood 5 late-pupa. For explanation of symbols see page 149



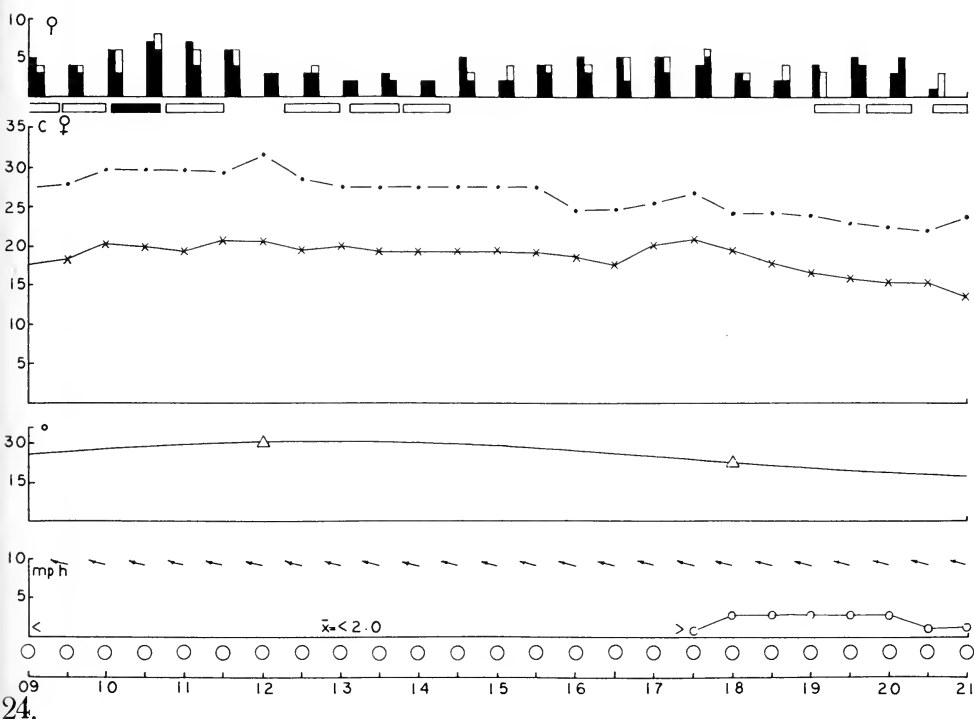
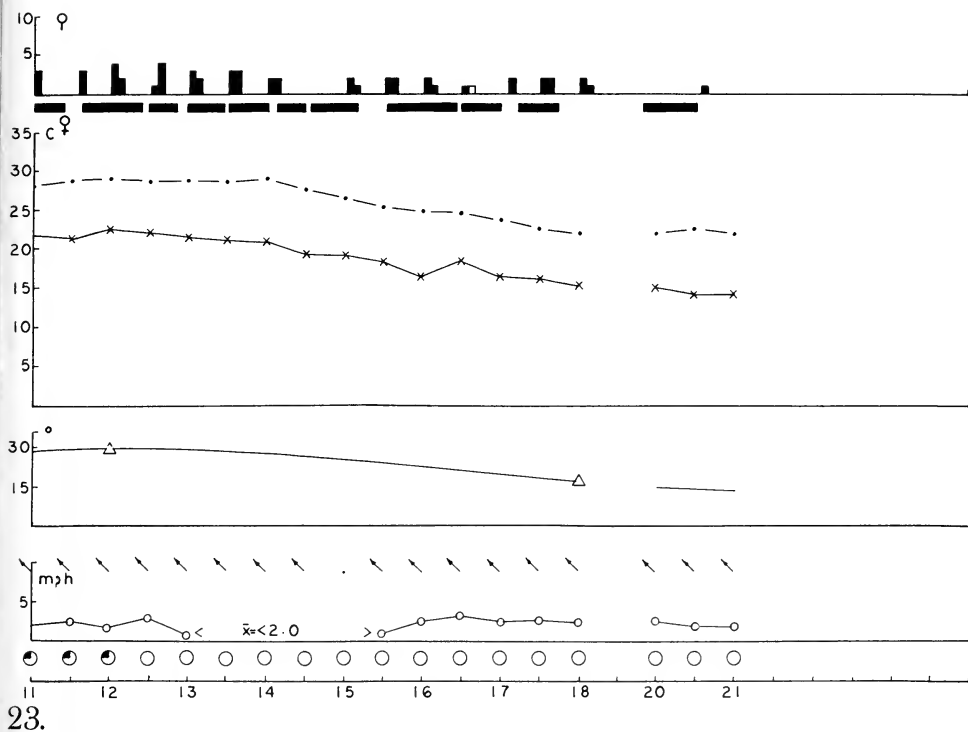


Fig. 23. July 9, 1968; one queen, 14 workers. Fig. 24. July 11, 1968, one queen, 14 workers. For explanation of symbols see page 149

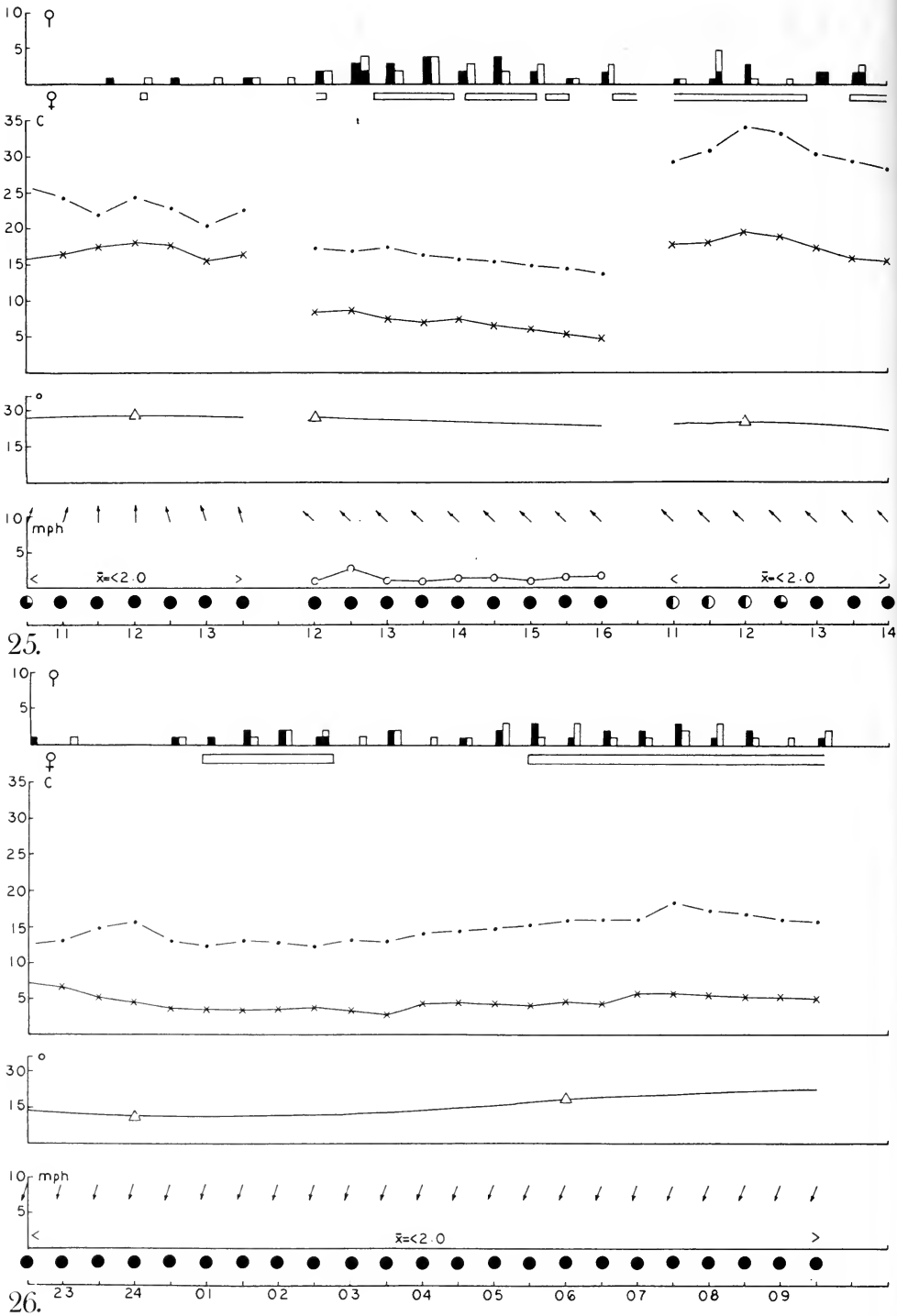


Fig. 25. July 14, 15, 19, 1968; one queen, 10 workers. Fig. 26. July 21, 1968; one queen, 8 workers. For explanation of symbols see page 149

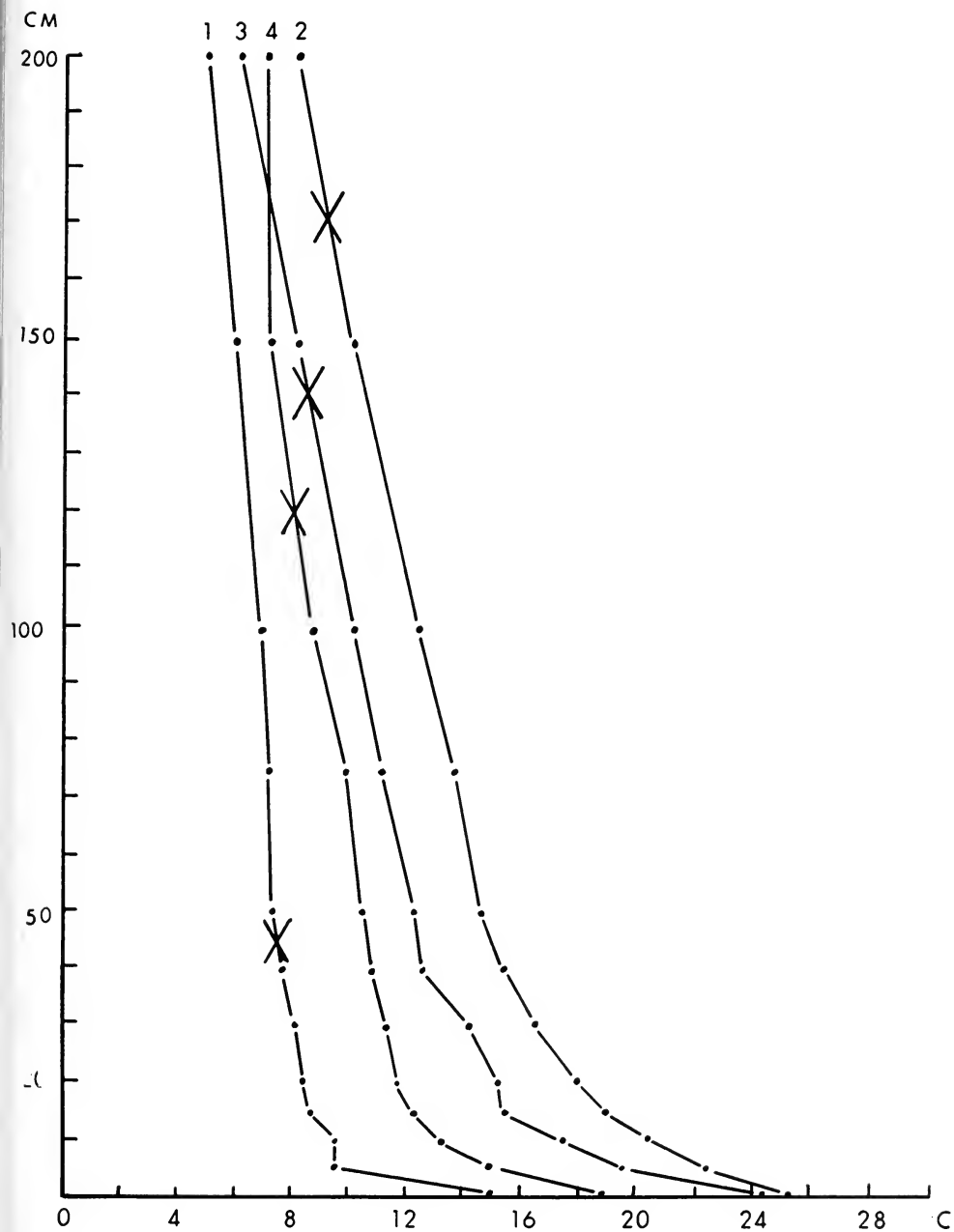


Fig. 27. Profile of air temperatures on 1. June 30, 2. July 5, 3. July 15, and 4. July 31, 1968. X—estimated mean height of flight of queens and workers.



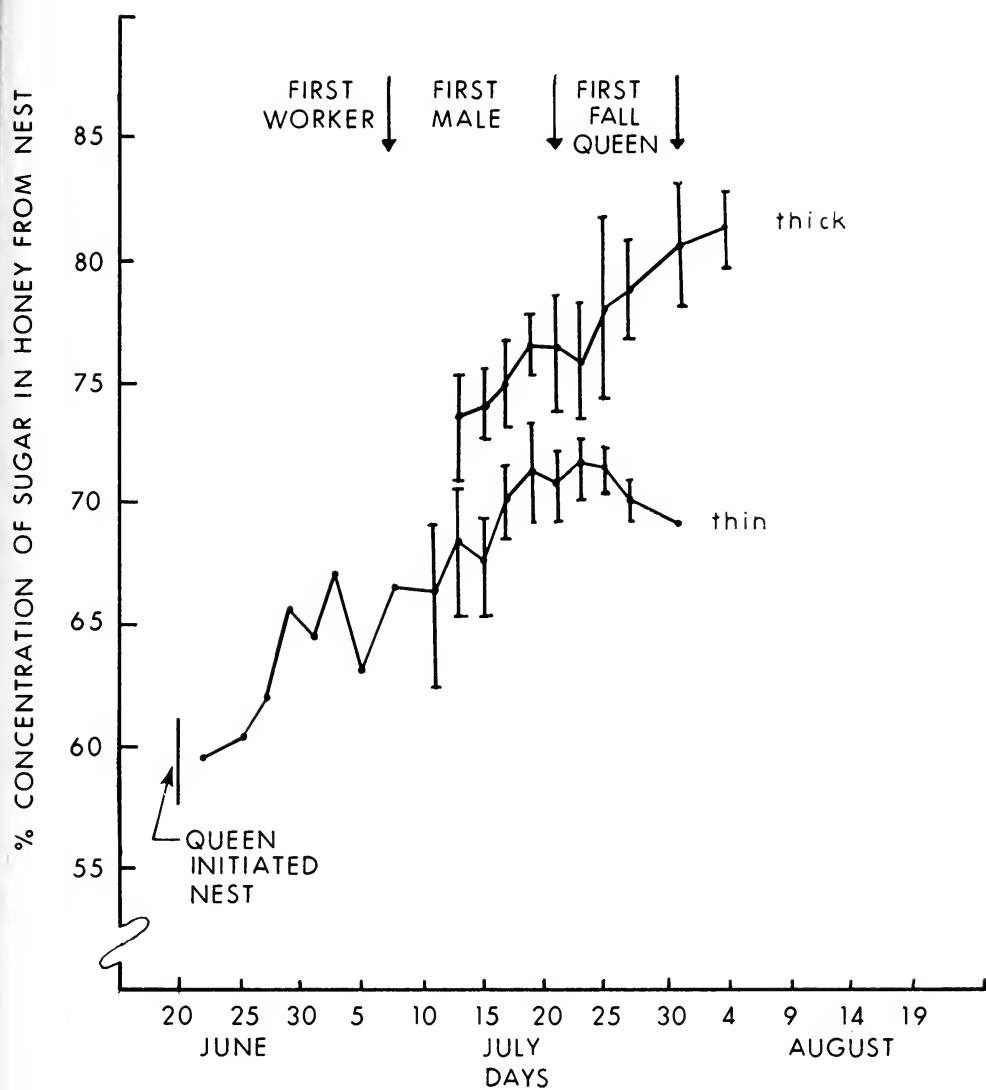


Fig. 29. The concentration of sugars from thin and thick honey from one nest. Vertical lines indicate one SD each side of mean. Arrows indicate first appearance of bees in nest.





Publication of *Quaestiones Entomologicae* was started in 1965 as part of a memorial project for Professor E. H. Strickland, the founder of the Department of Entomology at the University of Alberta in Edmonton in 1922.

It is intended to provide prompt low-cost publication for accounts of entomological research of greater than average length, with priority given to work in Professor Strickland's special fields of interest including entomology in Alberta, systematic work, and other papers based on work done at the University of Alberta.

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Volume 9

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## Editorial — Guess Whose Universe?

In 1967 Canada and Canadians spent lavishly to tell man that the world was his (Expo 67, Montreal — *Man and His World*; Quaest. ent. 4:33 *Man and whose world?*). Last year the United Nations, perhaps inspired by this example, conducted its Conference on the Human Environment - with a Canadian secretary general - in Stockholm. Any hopes we might have entertained that no possessive relationship between "Human" and "Environment" was intended in this title were early dispelled in the undated Canadian "Draft Declaration on the Human Environment" distributed in March 1972; nor were they subsequently restored by the responses to comments on this declaration, by the final Canadian submission to or report on the conference, nor by any of the meagre press comments on the conference either in Canada or in Australia.

The myth that man has his own environment, his own "fundamental right to adequate conditions of life" - accepted as part of Principle 1 at Stockholm, his own set of rules by which to live and survive, dies hard. It has been blamed on Christianity, but clearly dates back further than this and was perhaps a part of the dogma of most early religions. Noah was instructed to: "Be fruitful, and multiply ... and the fear of you and the dread of you shall be upon every beast of the earth, and upon every fowl of the air; with all wherewith the ground teemeth, and all the fishes of the sea, into your hand are they delivered."; his successors still act on this advice. Noah, however, was a propagule; survivor of a catastrophe. It was sound advice for him. His successors, if they follow the same advice, may generate one. Every ecologist knows that to accept a "fundamental right to adequate conditions of life" for man is to accept it for every other organism with which he interacts. Nobody, it seems, got up and said so at Stockholm.

In Principles 2 through 5 the Stockholm Conference averred that the natural resources of the earth must be safeguarded for the benefit of present and future generations. The capacity of the earth to produce vital renewable resources must, it agreed, be maintained and, *whenever practicable*, (italics ours) restored or improved. The non-renewable resources of the earth must be employed in such a way as to guard against the danger of their future exhaustion and to ensure that benefits from such employment are shared by all mankind. Yet all this is jettisoned in Principle 21 which declares that: "States have ... the sovereign right to *exploit* (italics ours) their own resources". Most overdeveloped countries endorsed these principles; all continue to condone, for example in the field of urban transportation, the use of 200 h.p. to transport one man when 1 h.p. can do this at the legal speed limit. N. American oil companies, directly and through their governments, are currently determined to get the fossil fuels out of the arctic for this generation; they are aided and abetted by each and every one of us when we say "fill 'er up." Our representatives endorsed these principles. There can rarely have been, outside the hard core of politics, so many forked tongues producing such a magnificent collection of double talk.

This conference has been acclaimed; but it bodes ill for the future, displaying as it does the same pompously inflated idea of the importance of man and especially N. American man as has led him to his present impasse with the rest of nature. It seems likely to lead to an international repetition of Man and his World. Then what? - Guess whose universe?

Brian Hocking

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*Quaestiones entomologicae*  
9:161-171 1973

*Locality records for 11 species, aestuans, ater, discalis, excitans, frigidus, fulvaster, furcatus, mitis, nigripes, noctifer pertinax, and zinzalus, are given. A key is provided for the identification of females.*

*Nous représentons la distribution de 11 espèces, aestuans, ater, discalis, excitans, frigidus, fulvaster, furcatus, mitis, nigripes, noctifer pertinax, et zinzalus. Une clef pour la détermination des femelles de ces espèces est pourvue.*

This paper assembles locality records for the Alberta species of *Chrysops* and provides diagnoses and a key for the identification of females. Eleven species are dealt with, of which one, *Chrysops zinzalus* Philip, is recorded from Alberta for the first time. Two species previously recorded from Alberta, *Chrysops callidus* Osten Sacken and *Chrysops proclivis* Osten Sacken, are omitted as I have been unable to trace any specimens of them from Alberta.

All descriptions and comments refer to females. The male of *C. zinzalus* is undescribed. The male of *Chrysops ater* Macquart was described by Philip (1955) as *Chrysops carbonarius nubiapex*. Descriptions of the males of all other species are in Brennan (1935).

Synonymies are recorded when there has been a change in status since Philip's (1965) catalogue; i.e. for *Chrysops ater*.

Figures 1 and 2 show the parts of the head and wings used in the diagnoses and key.

Localities are listed from east to west and south to north in areas limited by 1° of longitude and 1° of latitude.

## DIAGNOSTIC CHARACTERISTICS AND GEOGRAPHICAL DISTRIBUTION

### *Chrysops aestuans* Wulp, 1867

Females of this species are distinguished from those of other Alberta *Chrysops* by having a shiny yellow frontoclypeus, no pollinose stripe, and a very narrow apical spot on the wing (Fig. 3).

Females of *C. aestuans* are similar to those of *C. callidus* but the two taxa are distinguished by differences in abdominal and wing patterns. Females of *aestuans* have sublateral black triangles on the second abdominal tergum, and the apical spot is paler than the cross-band and one-half the width of cell R<sub>1</sub>. In females of *callidus* the sublateral marks, when present, are not triangles, and the apical spot is the same density as the cross-band and varies between one-half and the full width of cell R<sub>1</sub>.

*Chrysops aestuans* appears to be rare in Alberta (Fig. 16). I have seen two specimens from Miquelon Lake (June 21, July 20) and one in the Canadian National Collection labelled "Alberta". Strickland (1946) recorded a specimen from Wild Horse.

### *Chrysops ater* Macquart, 1850

*Chrysops ater* was described by Osten Sacken (1875) as *Chrysops fugax*, by Philip (1955) as *Chrysops carbonarius nubiapex*, and cited by Philip (1965) as a synonym of *Chrysops*

*carbonarius*. The specific name, *Chrysops ater*, was erected as the senior synonym by Pechuman and Burton (1969).

Females of *ater* are likely to be confused with those of *mitis*. They can be separated by their, usually, smaller size and the hyaline area at the proximal end of cell Cu<sub>1</sub> (Fig. 4). In females of *ater*, body length is from 7-9 mm and wing length  $8.06 \pm 0.47$  mm (mean  $\pm$  S.D.); while in *mitis* females, body length is from 8.5 - 11 mm and wing length  $9.44 \pm 0.41$  mm.

The distribution of *C. ater* in Alberta is shown in Fig. 15.

### Locality Records

Elkwater June 10-July 18 (CNC); Manyberries June 4 (CNC); Purple Springs June 18 (LLP); Lethbridge June 15-July 21 (CNC, UASM, LLP); Pincher July 10 (UASM); Cowley June 19 (CNC); Coleman reared (CNC); Medicine Hat June 12-July 16 (CNC); Hayes July 11 (CNC); Scandia July 9 (CNC); Milo July 1 (AWT); Hartell reared (AWT); Turner Valley reared (AWT); Calgary 35 miles sw June 16-18 (AWT); Calgary 20 miles w June 23 (CNC); Seebe June 10 (LLP); Menaik July 26 (UASM); Rocky Mountain House May 29 (UASM); Nordegg July 10-July 31 (AWT, UASM); Leduc July 7 (AWT); Edmonton May 30-June 9 (UASM); Edmonton 2 miles w June 12-20 (AWT); Wabamun reared (AWT), June (UASM); Lac La Biche June 30-July 5 (UASM); Athabasca 20 miles e June 30 (AWT); Flatbush June 22 (UASM); Westlock 14 miles s July 5 (AWT); Valleyview 45 miles sw June 17 (UASM); Calling Lake June 22 (UASM); Ft. McMurray June 6-26 (CNC); Manning 43 miles n July 12 (UASM); High Level 50 miles n July 10 (UASM).

### *Chrysops discalis* Williston, 1880

Females of this species are distinguished from those of other Alberta *Chrysops* by having a shiny yellow frontoclypeus (with 2 or 4 black spots) with a wide median pollinose stripe, and by their wing pattern (Fig. 5).

*Chrysops discalis* appears to be confined to the south-east portion of the province in the vicinity of alkaline lakes (Fig. 16).

### Locality Records

Orion August 9 (UASM); Lethbridge July (UASM); Medicine Hat July 14 (CNC); Scandia July 25 (CNC); Milo reared (AWT), June 30-July 11 (AWT); Consort July (UASM); Czar July 19 (UASM).

### *Chrysops excitans* Walker, 1850

Females of this species are the largest of the Alberta *Chrysops* species. Body length averages 11 mm and wing length  $10.07 \pm 0.23$  mm. Most females have the apex of the wing, beyond the cross-band, hyaline (Fig. 6), and extensive lateral yellow/orange areas on the first two or three abdominal terga. I have seen 5 females which differ from typical females in the following: body length ranges between 8-9 mm, the lateral pale areas on the abdomen are small, there are no mid-dorsal pale triangles on the abdomen, a vague infuscation is present in cell R<sub>1</sub> past the cross-band, and the anal cell is hyaline at its proximal end (Fig. 7). There are 56 similar specimens in the Canadian National Collection from various localities in Canada (Teskey, *in litt.*). Many workers, including Osten Sacken (1875), have remarked upon the great variation in abdominal colour pattern in specimens of *C. excitans*. However, Osten Sacken (1875) noted (p. 374) that the wing pattern was remarkably uniform in all specimens. Philip (1931) reported on the difference in eye pattern between the larger, typical females of *excitans* and the smaller darker specimens. I am not fully convinced that *C. excitans*, as presently understood, is monospecific.

The typical specimens are abundant in the northern and western parts of the province (Fig. 17) and readily attack man.

### Locality Records

Waterton Lakes June 27 (CNC); Pincher July 10 (UASM); Calgary 35 miles sw June 18 (AWT); Morley reared (CNC); Seebe reared (CNC), June 8-18 (CFS, CNC); Banff July 6 (CNC, LLP); Banff Pk. Eisenhower Jct. July 2-August 2 (CNC,

UASM); Lake Louise July 14 (CNC); Nordegg reared (AWT), June 24-August 3 (AWT); Jasper Pk. Honeymoon Lake August 11 (LLP); Jasper 7 miles w July 30 (LLP); Jasper Pk. Patricia Lake June 25 (LLP); Jasper July 28 (DMD); Edmonton July 24 (UASM); Edmonton 30 miles w June 15 (AWT); Fawcett June 20 (CNC, UASM, LLP); Flatbush June 16-19 (UASM); Smith July 14 (UASM); Slave Lake 20 miles se June 27-August 2 (AWT); Ft. McMurray June 11-27 (CNC); Ft. Chipewyan July 3 (CNC); 60°N June (UASM).

The small dark specimens were from Nordegg, Lac La Biche, Valleyview (45 miles SW) and Slave Lake (20 miles SE); collection dates were from June 17 to August 7.

### *Chrysops frigidus* Osten Sacken, 1875

Females of this small (6.5-8 mm long) black and yellow species are similar to those of *C. nigripes* and *C. zinzalus*. Colour varies, from some females having large sublateral yellow areas on abdominal terga 1 and 2 and predominantly yellow legs to females with the yellow areas reduced to small spots and the legs predominantly black. The large apical spot broadly attached to cross-band (Fig. 8) serves to distinguish females of *frigidus* from those of *nigripes* and *zinzalus*.

The distribution of *C. frigidus* in Alberta is shown in Fig. 18.

### Locality Records

Hartell reared (AWT); Calgary 35 miles sw June 17-August 9 (AWT); Morley reared (CNC); Banff July 11-27 (CNC, LLP); Banff Pk. Bow Summit July 21 (UASM); Nordegg July 21-August 10 (AWT); Opal June 23-August 9 (UASM); Edmonton 2 miles w reared (AWT), June 12-21 (AWT); Edmonton 30 miles w June 5-July 3 (AWT); Wabamun June 27 (UASM); Drayton Valley June 29 (UASM); Evansburg 6 miles nw June 19 (AWT); Lac La Biche June 29 (UASM); Athabasca 20 miles e June 30 (AWT); Westlock 14 miles s June 17-July 26 (AWT); Valleyview 45 miles sw June 17 (UASM); Slave Lake 20 miles se July 11-August 2 (AWT); High Level 40 miles s July 12 (UASM).

### *Chrysops fulvaster* Osten Sacken, 1877

Females of this species are distinguished from those of other Alberta *Chrysops* by their wing pattern (Fig. 9) and by having a yellow/orange spot on the frontal callus; in all other Alberta species of *Chrysops* the frontal callus is completely black.

The distribution of *Chrysops fulvaster* in Alberta is shown in Fig. 18.

### Locality Records

Lethbridge reared (CNC), July 14 (CNC); Cowley July (LLP); Medicine Hat July 8-23 (CNC, UASM); Milo July 11 (AWT); Consort July 18 (UASM); "Red Deer River" July 12 (CNC).

### *Chrysops furcatus* Walker, 1848

Females of this species are distinguished from those of other Alberta *Chrysops* by having a shiny yellow frontoclypeus, no pollinose stripe, and a broad apical spot separated from the cross-band (Fig. 10). Females of *C. proclivis* are similar to those of *C. furcatus* but can be separated from them by the completely infuscated cell R.

Dark females of *C. furcatus* were described by Philip (1955) as subspecies *chagnoni*. These differ from typical *furcatus* in having the antennae, fore coxae, and fore and hind femora black, and by having two isolated sublateral upright black dashes on the second abdominal tergum. In Alberta there is a full intergradation between typical *furcatus* and *chagnoni*. Recognition of the darker specimens of *furcatus* as *chagnoni* seems unnecessary. It is possible that Brennan's (1935) and Strickland's (1938) records of *C. proclivis* from Alberta refer to the dark form of *furcatus*.

The distribution of *C. furcatus* in Alberta is shown in Fig. 19.

### Locality Records

Waterton June 30 (CNC); Maycroft reared (CNC); Hartell reared (AWT); Turner Valley reared (AWT); Calgary 35 miles sw June 18-August 7 (AWT, UASM); Morley 8 miles e July 3 (CNC); Morley reared (CNC); Seebe reared (CNC), June 23-July

(CFS, CNC); Banff June 23-August 11 (CBP, CFS, CNC, UASM, LLP); Banff Pk. Eisenhower Jct. July 2-25 (UASM, CNC); Banff Pk. Moraine Lake August 16 (LLP); Nordegg reared (AWT), June 10-August 10 (AWT, CBP, CNC, UASM); Nordegg 35 miles sw reared (AWT); Jasper Pk. Sunwapta Falls July 28-29 (DMD); Jasper June 26-July 29 (CBP, UASM); Opal July 5 (UASM); Coronado June 23-July 22 (UASM); Edmonton June 7-July 24 (AWT, UASM); Devon July 3 (AWT); Golden Spike July 11 (UASM); Edmonton 30 miles w June 5-15 (AWT); Wabamun reared (AWT); Sundance July 8 (UASM); Evansburg 6 miles nw June 19 (AWT); Grande Cache reared (AWT); Westlock 14 miles s reared (AWT), June 18-July 26 (AWT); Lac La Biche July 6 (CFS); Athabasca 20 miles e June 30 (AWT); Fox Creek July 8 (UASM); Valleyview 45 miles sw June 17 (UASM); Athabasca 28 miles n June 22 (UASM); Hondo July 31 (AWT); Slave Lake 20 miles se July 5-August 2 (AWT); Ft. McMurray July 23 (CNC); Manning 15 miles n July 12 (UASM); Ft. Chipewyan July 5 (CNC).

### *Chrysops mitis* Osten Sacken, 1875

Females of *mitis* can be separated from those of *ater* (q.v.) by size, and by cell Cu<sub>1</sub> being infuscated at its proximal end (Fig. 11). Some females of *mitis* have grey mid-dorsal triangles on abdominal segments 2, 3, and 4.

The distribution of *C. mitis* in Alberta is shown in Fig. 20.

### Locality Records

Cypress Hills June 25-July (CNC, UASM); Elkwater June 10-July 20 (CNC); Aden June 28 (CNC); Taber June 27 (CBP); Lethbridge June 8-July 14 (CBP, CNC, UASM); Waterton larvae (Shamsuddin 1966), July 22 (CNC); Spring Point reared (CNC); Cowley June 16 (CNC); Maycroft reared (CNC); Frank June 15 (CNC); Medicine Hat June 14-July 8 (CNC, UASM); Vauxhall larvae (Shamsuddin 1966); Hartell reared (AWT); Turner Valley reared (AWT); Calgary 35 miles sw June 16-July 27 (AWT); Morley 15 miles e June 23-July 19 (CNC); Morley 8 miles e June 26 (CNC); Morley reared (CNC); Seebe reared (CNC), July 11 (CNC); Banff July 11-August 7 (CNC, LLP); Banff Pk. Johnston Canyon July 18 (CNC); Banff Pk. Eisenhower Jct. July 11-14 (CNC); Pine Lake July (UASM); Brazeau Dam July 9 (UASM); Nordegg July 7-August 10 (AWT, CNC, UASM, LLP); Opal June 23 (UASM); Millet June 6 (UASM); Leduc reared (AWT), July 7-11 (AWT); Edmonton June 23 (UASM); Edmonton 2 miles w June 11-July 7 (AWT); Wabamun reared (AWT), June 16-July 5 (AWT, UASM); Evansburg 6 miles nw June 19 (AWT); Lac La Biche July 14 (UASM); Athabasca 20 miles e June 30 (AWT); Clyde reared (AWT); Flatbush June 21 (UASM); Valleyview 45 miles sw June 17 (UASM); Calling Lake June 22 (UASM); Slave Lake 20 miles se June 27-July 20 (AWT); Ft. McMurray June 3-22 (CNC); Steen River July 11 (UASM).

### *Chrysops nigripes* Zetterstedt, 1838

Females of *nigripes* are distinguished from those of other Alberta species of *Chrysops* by wing pattern (Fig. 12), and by the characters given in the key.

I have seen two specimens of this holarctic species from Alberta. Both were collected by E. H. Strickland, July 20 and August 2, 1938. Philip (*in litt.*) has a female collected by Strickland, July 8 1931; Pechuman has seen a female collected July 9. All Alberta records are from Wabamun (Fig. 21). This population is now probably extinct. The report of *C. nigripes* from Nordegg (Thomas 1970) was erroneous; the specimen is a female of *C. zinzalus*.

### *Chrysops noctifer pertinax* Williston, 1877

Brennan (1935) considered *Chrysops noctifer* Osten Sacken and *C. pertinax* to be specifically distinct.

The black body together with the distinct apical spot on the wing (Fig. 13) serves to distinguish *C. n. pertinax* females from females of the other Alberta *Chrysops* species.

This species has been collected, in Alberta, in the mountains in the south-west portion of the province (Fig. 22).

### Locality Records

Waterton June 25-July (CDA, CNC, UASM); Waterton Pk. Cameron Lake June 19 (CNC); Seebe July 11 (CNC); Banff June 23-August 7 (CNC, UASM, LLP); Banff Pk. Eisenhower Jct. July 2-August 2 (CNC, UASM); Banff Pk. Lake Louise July 14 (CNC); Banff Pk. Bow Summit July 21 (UASM).

### *Chrysops zinzalus* Philip, 1942

Females of this species resemble those of *nigripes* and the darkest females of *frigidus*. The apical spot dilated beyond the cross-band and the hyaline area at the proximal angle of the



discal cell (Fig. 14), and the convex upper corners of the frontal callus (Fig. 1) separate females of *zinzalus* from those of *nigripes*. Females of *zinzalus* are distinguished from dark females of *frigidus* by wing pattern and the completely black hind tibiae.

Pechuman (1972) discussed the status of *C. zinzalus* suggesting that it could be a variant of *C. nigripes*. He had seen all of the then known 16 specimens of *zinzalus* (all from north-east North America). Only one of these matched the holotype in lacking a projection from the outer margin of the cross-band toward the base of vein  $R_4$ . I have 7 females, all of which possess a projection from the cross-band (Fig. 14). Since the observation by Philip (*in litt.*, March 1973) that females of *zinzalus* have a hyaline spot at the proximal end of the discal cell, there can be little doubt as to the distinctiveness of *Chrysops zinzalus*.

The 7 females I have were all collected in Manitoba fly traps in *Sphagnum* bogs. Six came from Nordegg, July 20-31; and one from 20 miles south-east of Slave Lake, August 2 (Fig. 21).

#### KEY TO THE FEMALE *CHRYSOPS* OF ALBERTA

1. Frontoclypeus shiny black with median yellow pollinose stripe . . . . . 2
- Frontoclypeus shiny yellow, with or without stripe. . . . . 8
2. Apical spot on wing distinct. . . . . 3
- Apical spot absent, vague infuscation in a few specimens. . . . . 6
3. Hyaline triangle extends to costa; colour black. . . . . *noctifer pertinax*
- Hyaline triangle not extending across vein  $R_{2+3}$ ; not completely black . . . . . 4
4. Hyaline triangle, at most, extends across bifurcation of veins  $R_4$  and  $R_5$ ; legs often predominantly yellow . . . . . *frigidus*
- Hyaline triangle extends to vein  $R_{2+3}$ ; legs predominantly black. . . . . 5
5. Apical spot not wider than cell  $R_1$ ; proximal angle of discal cell infuscated; upper corners of frontal callus in form of right angles . . . . . *nigripes*
- Apical spot dilated beyond cross-band; proximal angle of discal cell hyaline; upper corners of frontal callus convex. . . . . *zinzalus*
6. Abdominal terga 1 and 2 with yellow/orange sublateral areas . . . . . *excitans*
- Abdomen black, with greyish pollinose areas in some specimens . . . . . 7
7. Cell  $Cu_1$  with distinct or obscure hyaline spot at proximal end . . . . . *ater*
- Cell  $Cu_1$  without hyaline spot . . . . . *mitis*
8. Frontoclypeus with pollinose stripe; cell  $R_5$  infuscated at wing margin . . . . . 9
- Frontoclypeus without stripe; cell  $R_5$  hyaline beyond cross-band . . . . . 10
9. Frontal callus completely black; cell 2nd. M hyaline . . . . . *discalis*
- Frontal callus with orange spot; cell 2nd. M about 1/2 infuscated . . . . . *fulvaster*
10. Cell R predominantly hyaline; apical spot narrow . . . . . *aestuans*
- Cell R predominantly infuscated; apical spot broad. . . . . *furcatus*

#### ACKNOWLEDGEMENTS

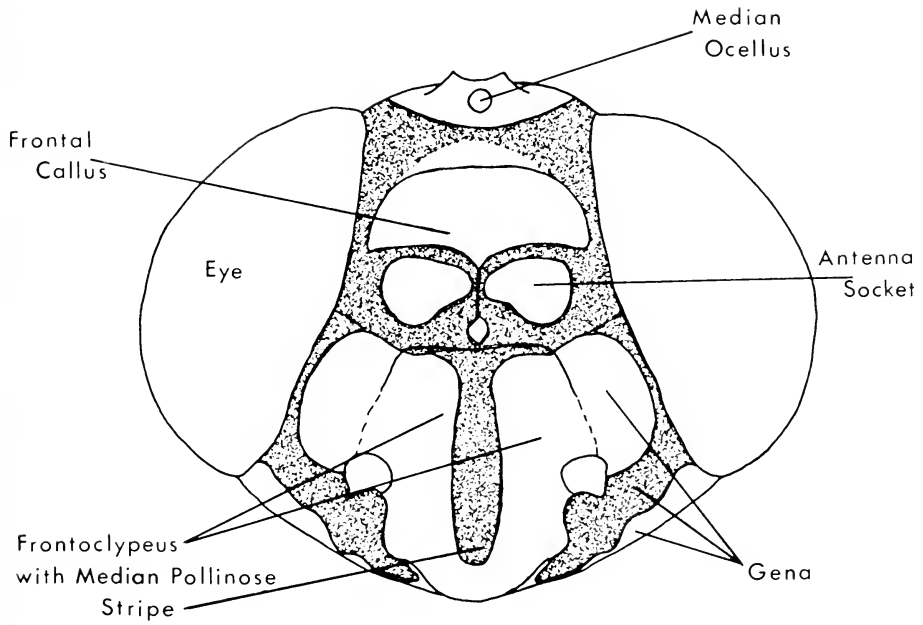
I am indebted to the following for allowing me to examine the collections in their institutions: G. E. Ball, Curator, E. H. Strickland Museum (UASM), Department of Entomology, University of Alberta; L. Burgess, C.D.A. Research Laboratory (CDA), Saskatoon; J. Melvin, Department of the Environment, Canada Forestry Service (CFS), Edmonton; H. J. Teskey, Diptera Section, Entomology Research Institute, Canadian National Collection (CNC), Ottawa. D. M. Davies (DMD), L. L. Pechuman (LLP), and C. B. Philip (CBP) kindly made available their records of Alberta tabanids. Material I collected myself is so indicated (AWT). I

am especially grateful to L. L. Pechuman for his opinions on the composition and distribution of the Alberta tabanid fauna; and to both L. L. Pechuman and C. B. Philip for their help with the identification of *C. zinzalus*. My colleagues at the University of Alberta collected many specimens during the course of their own studies. I thank them all.

I thank G. E. Ball and H. J. Teskey for their criticisms of this manuscript, and J. Scott for assistance with the photography.

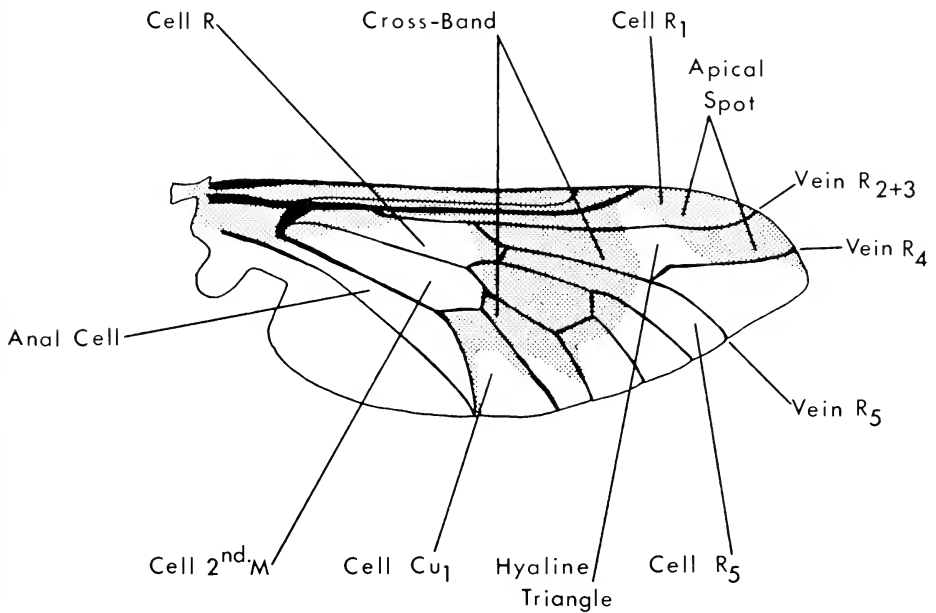
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①

Fig. 1. Anterior view of the head of a female *Chrysops zinzalus*; antennae and mouth parts removed.



②

Fig. 2. Right wing of a female *Chrysops furcatus* showing names assigned to those cells and veins used in this paper.

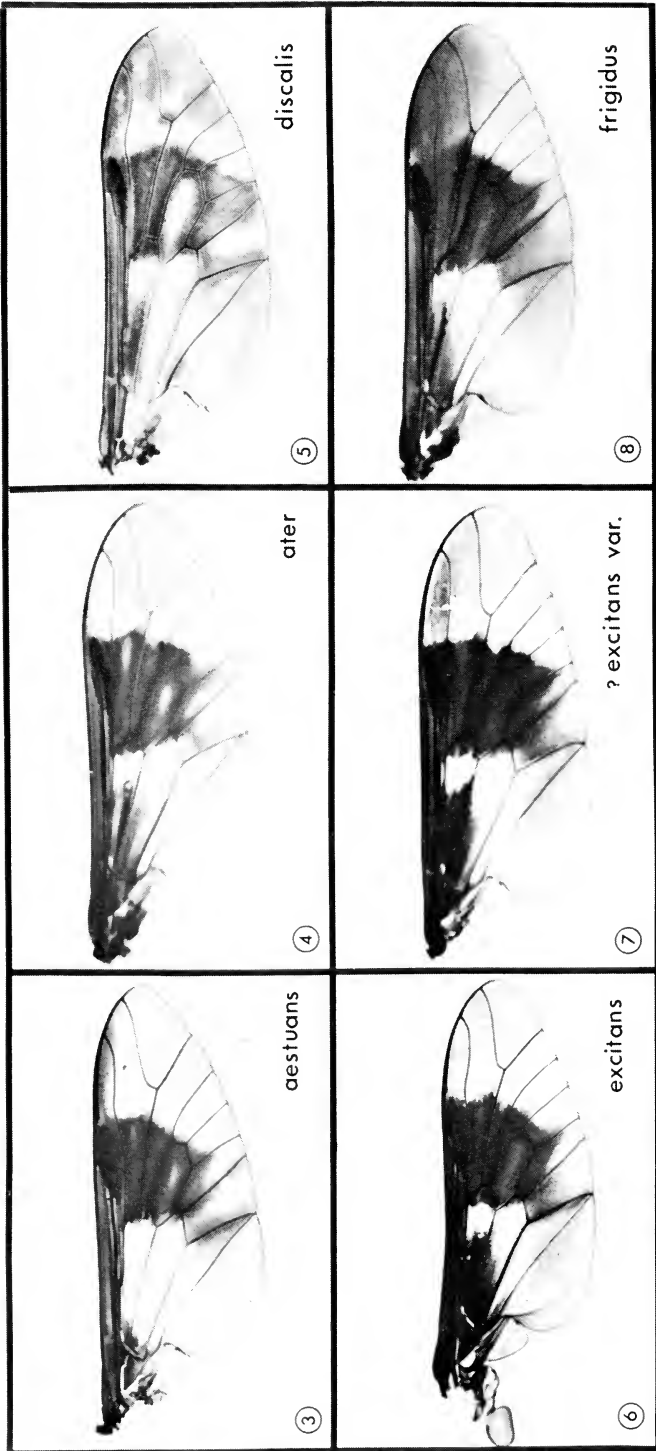


Fig. 3-8. Wings of females of *Chrysops aestuans*, *C. ater*, *C. discalis*, *C. excitans*, ? *C. excitans* var., and *C. frigidus*.

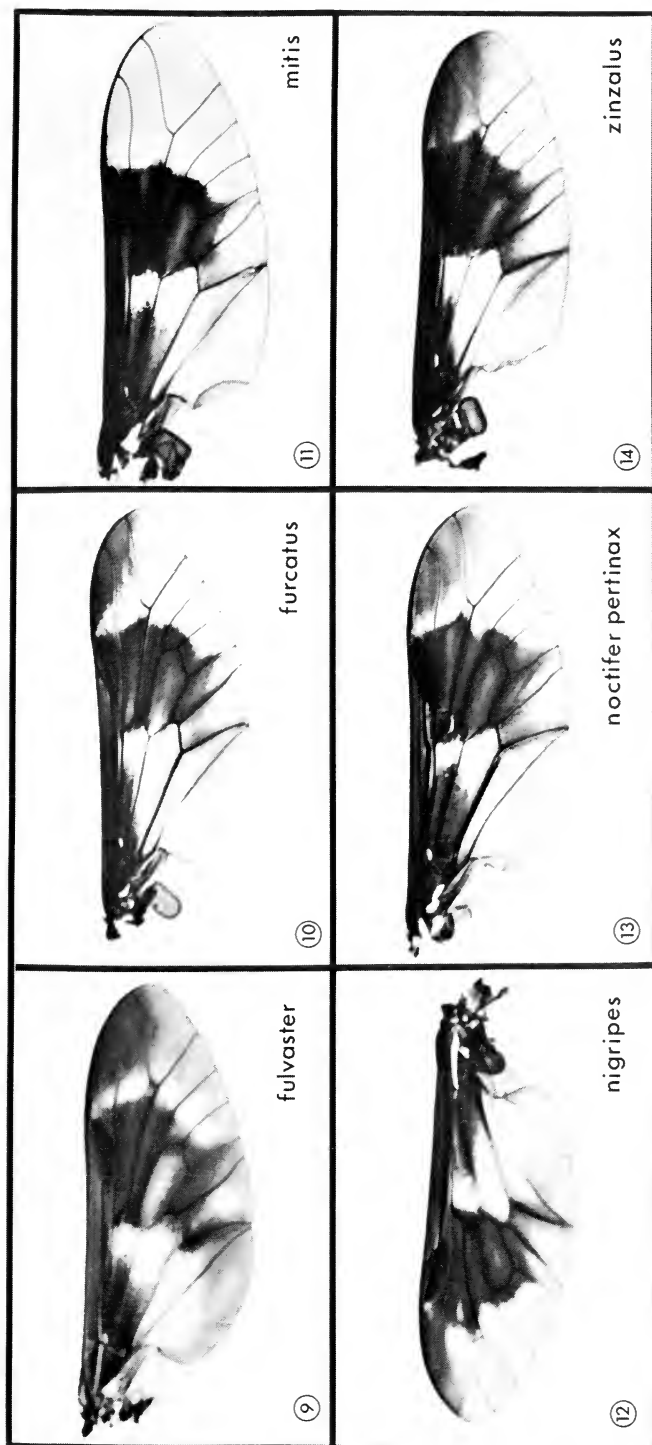


Fig. 9-14. Wings of females of *Chrysops fulvaster*, *C. furcatus*, *C. mitis*, *C. nigripes*, *C. noctifer pertinax*, and *C. zinzalus*.

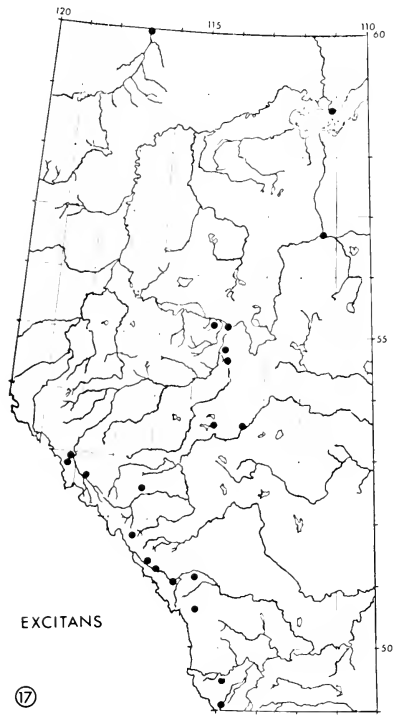
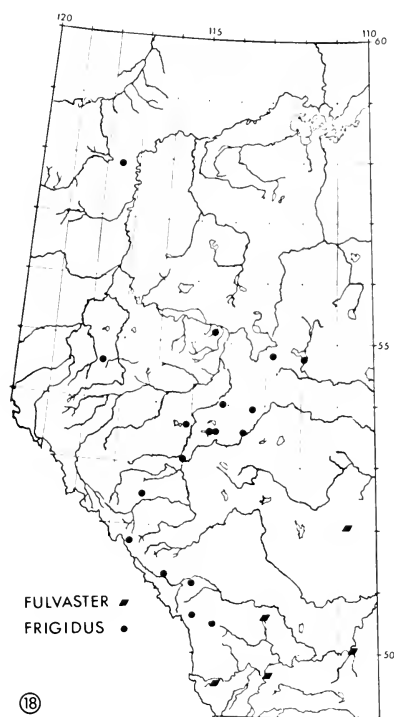
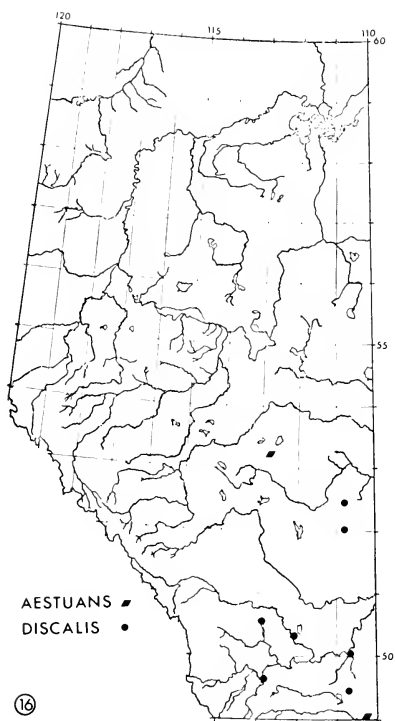
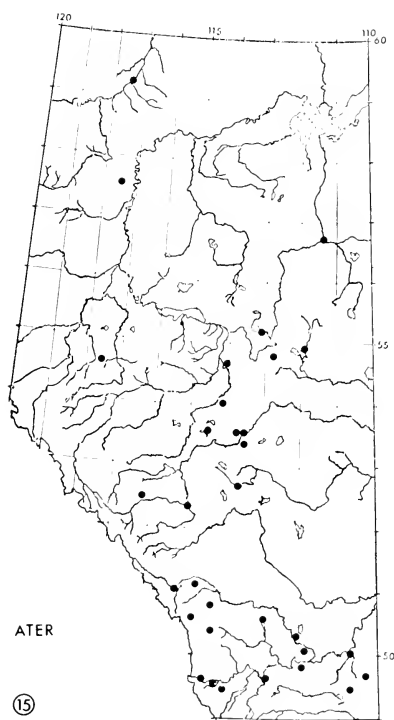


Fig. 15-18. Alberta distributions of *Chrysops ater*, *C. aestuans*, *C. discalis*, *C. excitans*, *C. fulvaster*, and *C. frigidus*.

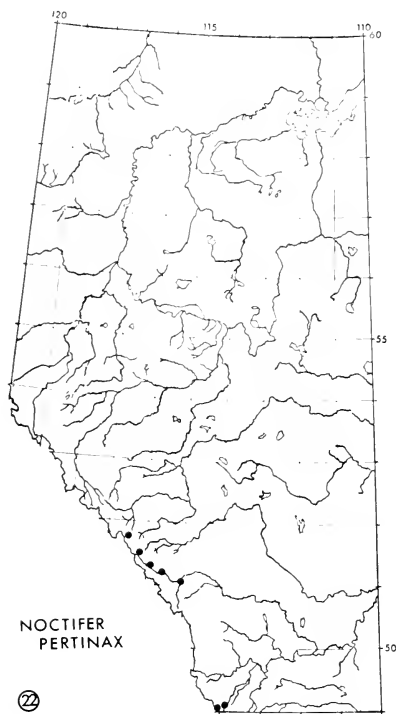
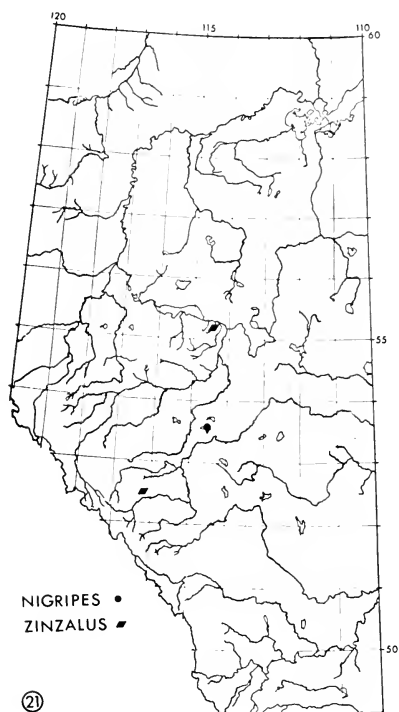
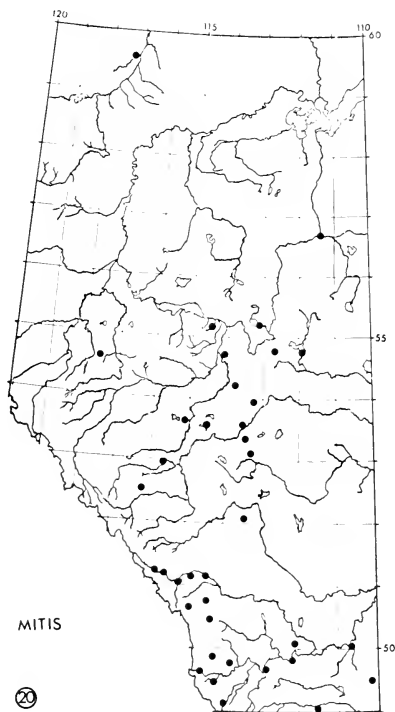
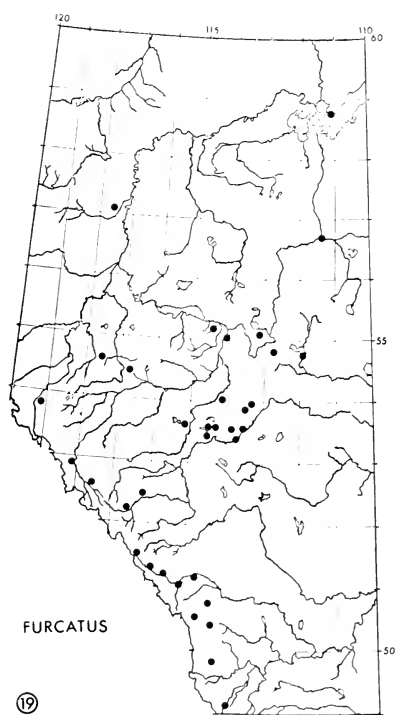
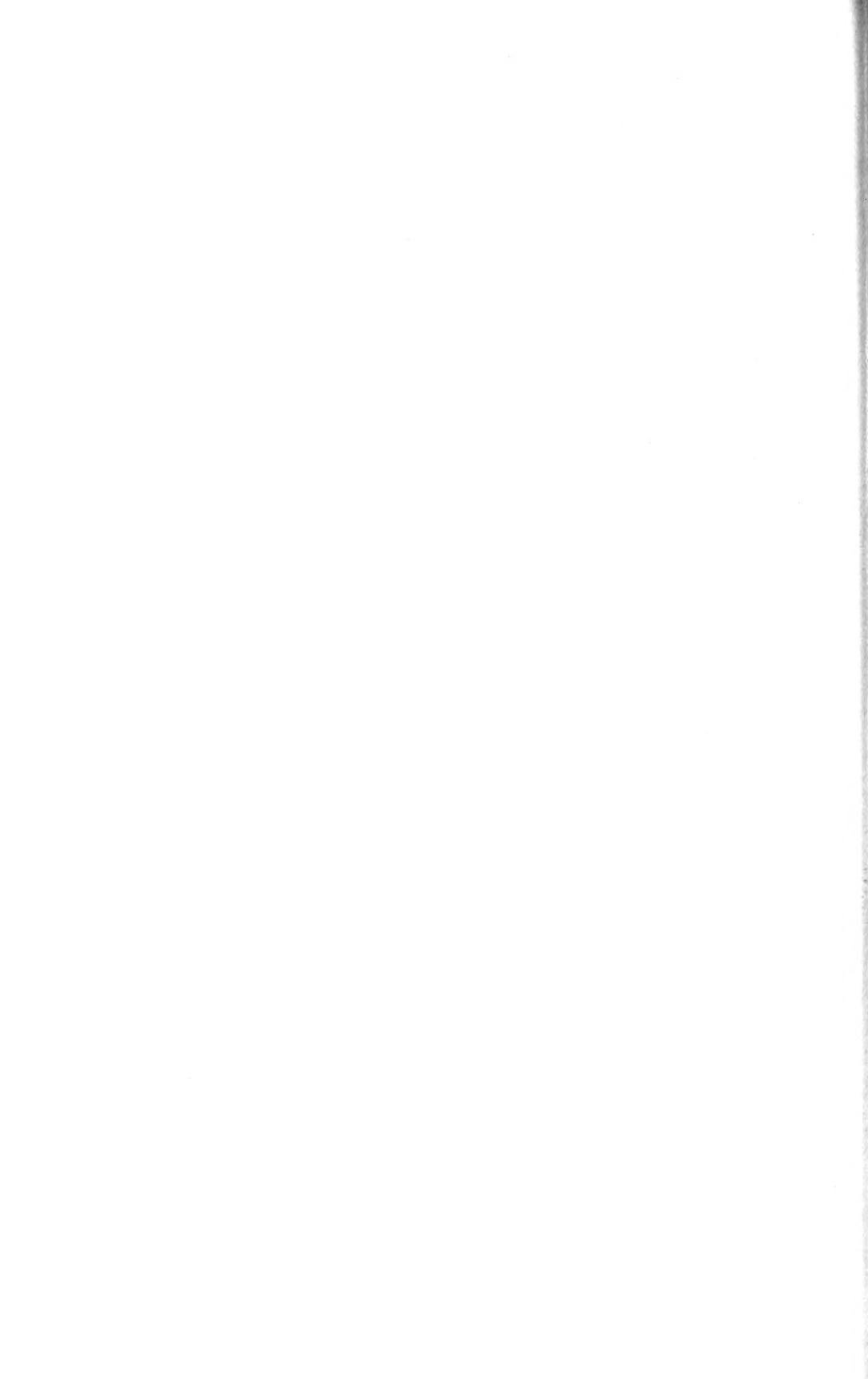


Fig. 19-22. Alberta distributions of *Chrysops furcatus*, *C. mitis*, *C. nigripes*, *C. zinzalus*, and *C. noctifer pertinax*.





ANNOTATED KEY TO PLATYNUS, INCLUDING MEXISPHODRUS AND MOST  
"COLPODES", SO FAR DESCRIBED FROM NORTH AMERICA INCLUDING MEXICO  
(COLEOPTERA: CARABIDAE: AGONINI).

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*Quaestiones entomologicae*  
9: 173-217 1973

The genus-group name *Platynus Bonelli* is resurrected and redefined to include certain taxa from Mexico and northward heretofore placed in *Agonum Bonelli* and *Colpodes MacLeay*. So constituted, *Platynus* further includes forms described in *Bolivaridius*, *Dyscolus*, *Mexispodrus*, *Ophryodactylus*, *Platynella*, *Rhadine*, *Stenocnemus*, and several other genus-group taxa. All members of the genus so far described from Mexico and southern Arizona, except cavernicolous members of the subgenus *Rhadine*, are distinguished from one another and from other Nearctic species groups in an annotated key.

I discuss 169 species-group names; designate lectotypes for 107 of them, including nine which were selected by G. E. Ball and one by R. B. Madge; assign these 169 names to 132 species here recognized; and place these 132 species in *Platynus*, all but three as new combinations. Of the 132 species recognized, four from Guatemala and two from South America receive brief mention in the text but are not keyed. *Colpodes approximatus* Chaudoir is noted for the first time as a member of the U.S.A. fauna, and is considered a junior synonym of *Platynus tenuicollis* LeConte.

The *Platynus* fauna of Mexico includes 125 described species; these are keyed to distinguish them both from one another and from as yet undescribed forms. Three species are re-named, as the old names are preoccupied in *Platynus* and lack available synonyms: *P. colibor*, new name for *P. bicolor* Chaudoir nec LeConte; *P. ilagis*, new name for *P. agilis* Chaudoir nec LeConte; and *P. lifragis*, new name for *P. fragilis* Chaudoir nec LeConte. Of 37 names for Mexican and Sonoran taxa here placed in synonymy, 25 are new synonymies: *P. championi* Bates (= *P. euides* Bates); *P. concisus* Bates (= *P. suffectus* Bates, = *P. petilus* Bates); *P. cupripennis* Laporte (= *P. cyanipennis* Chaudoir, = *P. nebrionides* Chaudoir); *P. cycloderus* Chaudoir (= *P. prolongatus* Bates, = *P. versicolor* Motschoulsky); *P. fratellus* Chaudoir (= *P. jalapensis* Bates, = *P. trujilloi* Bates); *P. lyratus* Chaudoir (= *P. pinalicus* Casey); *P. megalops* Bates (= *P. longiceps* Schaeffer); *P. moestus* Dejean (= *P. curtipennis* Casey); *P. monachus* Dejean (= *P. chloreus* Bates); *P. nitidus* Chaudoir (= *P. stenos* Bates, = *P. morelosensis* Casey, = *P. infidus* Casey); *P. nugax* Bates (= *P. simplicior* Bates, = *P. lymphaticus* Casey); *P. obscurellus* Bates (= *P. atratus* Chaudoir not Blanchard, = *P. incommodus* Chaudoir, = *P. harfordi* Casey); *P. procephalus* Bates (= *P. hondurae* Bates); *P. rectilineus* Bates (= *P. recticollis* Casey); *P. transversicollis* Chaudoir (= *P. unilobatus* Bates); and *P. variabilis* Chaudoir (= *P. guerrensis* Casey).

El grupo genérico *Platynus Bonelli* es redescubierto y redefinido a manera de incluir algunos taxa de Mexico y de los Estados Unidos que anteriormente fueron atribuidos a los generos *Agonum Bonelli* y *Colpodes MacLeay*. Así constituido, *Platynus* contiene ademas algunos taxa antes descritos como *Bolivaridius*, *Dyscolus*, *Mexispodrus*, *Ophryodactylus*, *Platynella*, *Rhadine*, *Stenocnemus*, a la vez que algunos otros géneros y subgéneros. Todos los miembros de este género descritos hasta ahora y localizados en Mexico y en el sur de Arizona, se distinguen mutuamente y de otros grupos de especies neárticas en una clave anotada, con exepcion de los miembros cavernícolas del subgénero *Rhadine*.

*Yo discuto 169 nombres; disigno 107 lectotipos, incluyendo nueve que fueron seleccionados anteriormente por G. E. Ball y uno por R. B. Madge; asigno además estos 169 nombres a 132 especies que fueron reconocidas; aquí, e incluyo estas 132 especies en el género Platynus, 129 como combinaciones nuevas. De las 132 especies reconocidas, cuatro de Guatemala y dos de Sur America son brevemente mencionadas en el texto pero no son tratados en la clave. La especie Colpodes approximatus Chaudoir es discutida por primera vez como miembro de la fauna de los Estados Unidos, y se considera como sinónimo subordinado de Platynus tenuicollis LeConte.*

*La fauna de Platynus en Mexico contiene 125 especies descritas; estas son puestas en clave para poderlas distinguir entre si además de entre otras especies no descritas hasta ahora. Tres especies son renombradas, porque los nombres originales están ya ocupados en Platynus y por la falta de sinónimos válidos: P. colibor, n.n. por P. bicolor Chaudoir nec LeConte; P. ilagis, n.n. por P. agilis Chaudoir nec LeConte; y P. lifragis, n.n. por P. fragilis Chaudoir nec LeConte. De los 37 nombres de taxa de Mexico y de Arizona aquí tratados como sinónimos, 25 son sinonimias nuevas: P. championi Bates (= P. euides Bates); P. concisus Bates (= P. suffectus Bates, = P. petilus Bates); P. cupripennis Laporte (= P. cyanipennis Chaudoir, = P. nebrionides Chaudoir); P. cycloderus Chaudoir (= P. prolongatus Bates, = P. versicolor Motschoulsky); P. fratellus Chaudoir (= P. jalapensis Bates, = P. trujilloi Bates); P. lyratus Chaudoir (= P. pinalicus Casey); P. megalops Bates (= P. longiceps Schaeffer); P. moestus Dejean (= P. curtipennis Casey); P. monachus Dejean (= P. chloreus Bates); P. nitidus Chaudoir (= P. stenos Bates, = P. morelosensis Casey, = P. infidus Casey); P. nugax Bates (= P. simplicior Bates, = P. lymphaticus Casey); P. obscurellus Bates (= P. atratus Chaudoir nec Blanchard, = P. incommodus Chaudoir, = P. harfordi Casey); P. procephalus Bates (= P. hondurae Bates); P. rectilineus Bates (= P. recticollis Casey); P. transversicollis Chaudoir (= P. unilobatus Bates); y P. variabilis Chaudoir (= P. guerrensis Casey).*

Several recent studies have appeared on Mexican Agonini (Agoni, *sensu* Lindroth, 1966): Barr, 1965, 1966, 1970; Barr *et al.*, 1968; Bolivar, 1944; Bolivar and Hendrichs, 1964, 1965; Straneo, 1957. Most of these concern cavernicolous or high altitude forms, as most original descriptions and early keys do not clearly distinguish the many low altitude epigeal and arboreal species. I have examined type material in the British Museum (Natural History) (London: BMNH), California Academy of Sciences (San Francisco: CAS), Institut Royal des Sciences Naturelles de Belgique (Brussels: IRSB), Museum of Comparative Zoology (Cambridge: MCZ), Museum National d'Histoire Naturelle (Paris: MNHP), and the United States National Museum (Washington: USNM). These studies facilitated identifications of nearly all Mexican Agoni described by earlier workers, and thus of nearly all epigeal forms.

Preliminary studies of adult morphology suggest that generic affinities within the Agoni require refinement. This is confirmed from comparisons of various agonine larvae (H. Goulet, *in litt.*): *Sericoda*, *Agonum s. str.*, *Colpodes bromeliarum* group of Jamaica, *Agonum decentis* group, and *Europhilus*. I think *Platynus*, including *Agonum decentis* group, *Agonum hypolithos* group, *Agonum larvale* group, most Mexican *Colpodes*, *Mexisphodrus*, and *Agonum* subgenus *Platynella* should be treated as a genus distinct from *Agonum*, as provisionally done in this paper. I am not sure precisely how to treat the *Agonum puncticeps* group; nor am I sure that *Platynus* should really include all of the Mexican "*Colpodes*". Perhaps additional genera are required. But it is evident that the type of *Colpodes*, *C. brunneus* MacLeay from Java, is congeneric with Mexican "*Colpodes*" only in a sense expanded to include all of these as elements of *Platynus*, an older name.

In this paper I treat as *Platynus* that segment of *Agonum* (*sensu* Lindroth) comprising the *decentis*, *hypolithos*, and *larvale* groups in America north of Mexico, i.e., the old subgenera *Platynus*, *Platynidius*, and *Rhadine*, respectively. I more specifically treat those Mexican forms which clearly are related to those groups, including most species listed as *Colpodes* and some as *Agonum* by Blackwelder (1944). I exclude those forms characterized by: parameres of male genitalia with terminal setae (*Elliptoleus*, *Sericoda*); anterior tibia externally canaliculate and male genitalia melanistic (*Glyptolenus*); or tarsal claws pectinate (*Onypterygia*). Members of *Cyrtolaus* may be related to forms treated here but are distinguished by: male endophallus with large distal sclerite; and by combination of tarsi strigose above, mouthparts greatly elongated, elytra fused, and stria punctures foveate. This genus and the pterostichine *Ithytolus* may be related (G. E. Ball, *in litt.*), as members of *Cyrtolaus* are distinguished mainly by external elytral plica absent. Also excluded are those elements of *Agonum* and *Europhilus* with male genitalia melanistic (except in some depigmented species), article four of front tarsus emarginate rather than lobate, and head not constricted behind eyes. All forms treated in this paper probably share a common ancestry remote from that of excluded forms except, perhaps, that of ancestral *Onypterygia*.

Thus restricted, I treat all names proposed for Mexican *Platynus* species through 1966 and at least some through 1970, though names for cavernicolous species of *Rhadine* are not discussed in detail. Other "*Colpodes*" reported from Mexico but not treated here do not belong to this section of the Agoni. My treatment of *Platynus* from America north of Mexico is but a slight extension of that of Lindroth; I do not discuss or key individual species included in his work except for *P. tenuicollis*, and I do not consider any of the subgenus *Rhadine*. I also omit the Asiatic species *Colpodes buehneri* Hope, which has been introduced into northwestern North America (see Hatch, 1953).

This paper comprises two main parts. I give a key to described species-group taxa; additional characteristics [in brackets!] distinguish specimens of described species from specimens of undescribed forms. This key is cumbersome in places, and should be used with caution. Individual specimens may not key readily through certain major couplets, and may require testing through both alternatives.

Following the key is an alphabetically arranged annotated list of taxa not treated by Lindroth (1966), with major literature citations, synonymies, type and lectotype designations, and descriptive, distributional, and comparative comments as appropriate. A statement to the effect that a species is "highly distinctive" means that, to my knowledge, there should be no problems in species recognition: no taxonomic problems are evident. With few exceptions, I do not restrict type localities, except as indicated by labels on lectotype specimens. Original type locality designations are given "in quotes!". I include notes on some Middle and South American species which may be found in Mexico, or which have erroneously been reported from there.

In selections of lectotypes for Chaudoir names, I exclude specimens in the Oberthür collection (MNHP) labelled "Ex Musaeo Sallé 1897" because Chaudoir may not have examined them. This matter will be explored further by G. E. Ball in a forthcoming paper on type specimens of other Mexican Carabidae.

Most types in MNHP are contained in the main body of the Oberthür collection, and for most I indicate box number, column, and row (e.g., 265/3/4). Types of some species described by Bates are in the separate Bates collection, and are noted as "Bates, MNHP". Some lectotypes were selected by G. E. Ball or R. B. Madge, and as designated in this paper are so credited.

## Key to species

- 1      Tempora strongly swollen; hind femur without subapical setae; tarsi strigose above; pronotal base trisinate (species key after Barr, 1970). . . . . 2
- 1'     Tempora not strongly swollen; [antennal article three not pubescent, or hind femur with subapical setae] . . . . . 4
- 2 (1)   Pronotum nearly as long as wide; head constricted behind eyes . . . . . 3
- 2'     Pronotum about 0.75 as long as wide; head not constricted behind eyes . . . . . *Platynus (Platynella) tolucensis* (Straneo).
- 3 (2)   Eye diameter less than length of scape; lateral pronotal explanation strongly reflexed; elytral apex angulate . . . . . *Platynus (Platynella) districtus* (Casey).
- 3'     Eye diameter and scape length subequal; lateral pronotal explanation less strongly reflexed; elytral apex less produced. . *Platynus (Platynella) montezumae* (Bates).
- 4 (1')   Punctures of elytral interval three strongly foveate; elytron not metallic . . . . . *Platynus cavatus* (Bates).
- 4'     Punctures of elytral interval three not strongly foveate, OR elytron metallic. . 5
- 5 (4')   Tarsi pubescent above; pronotal hind angle sharp; [body piceous]. . . . . *Platynus omaseoides* (Bates).
- 5'     Tarsi glabrous above, or pronotal hind angle rounded . . . . . 6
- 6 (5')   All or most males with more than one pair of anal setae, AND/OR all or most females with more than two pairs of anal setae (some species are quite variable in this characteristic, and are keyed through both alternatives; individual specimens of other species may require testing through both alternatives) . . . . . 7
- 6'     All or most males with one pair of anal setae, and all or most females with two pairs of anal setae. . . . . 26
- 7 (6)   Metepisternum short; hind femur of most specimens without dorsoapical setae; article five of hind tarsus ciliate beneath; internal sulcus of basal article of hind tarsus indistinct; pronotal hind angle prominent, lateral margin sinuate, lateral explanation reflexed; article four of hind tarsus emarginate, symmetric; prosternum not truncate; mentum tooth bifid; north of Arizona (*Platynus ovipennis* group, = *Platynus hypolithos* group in part; included species are *Platynus ovipennis* Mann-erheim and (?) *P. agilis* LeConte) . . . . . see Lindroth, 1966.
- 7'     Combination of characters not as above; Arizona and southward . . . . . 8
- 8 (7')   Lateral pronotal explanation narrow, lateral margin distinctly sinuate before hind angle, OR posterior pronotal seta absent. lateral pronotal margin not plurisetose . . . . . 9
- 8'     Lateral pronotal explanation broad, not reflexed, side margin not strongly sinuate OR hind angle rounded and setose; lateral pronotal margin plurisetose or not . 17
- 9 (8)   Posterior pronotal seta absent, anterior pronotal seta present . . . . . 10
- 9'     Posterior pronotal seta present, anterior pronotal seta present or absent. . . 11
- 10 (9)   Elytron submetallic; metepisternum short . . . . . 63
- 10'     Elytron black; metepisternum elongate . . . . . 11
- 11 (9'10') Flytron blue, head and pronotum rufous . . . . . *Platynus acuminatus* (Chevrolat).
- 11'     Elytron, head, and pronotum concolorous . . . . . 12
- 12 (11') Black, legs pale, AND elytral apex acuminate . . *Platynus pallidipes* (Chaudoir).
- 12'     Legs dark, OR elytral apex not markedly acuminate . . . . . 13
- 13 (12') Elytral microsculpture isodiametric; elytron strongly submetallic or not. . . 14
- 13'     Elytral microsculpture stretched; elytron not strongly submetallic . . . . . 15

- 14 (13) Strongly submetallic; [hind femur with one short subapical seta, or none]. . . . . *Platynus delicatulus* (Chaudoir).
- 14' Piceous, not submetallic; [posterior pronotal seta absent]. . . . . *Platynus semiopacus* (Chaudoir).
- 15 (13') Elytral microsculpture of distinct meshes . . . . . 16
- 15' Elytral microsculpture more stretched, not of distinct meshes; [legs dark; pronotal base impunctate]. . . . . *Platynus melanocnemis* (Chaudoir).
- 16 (15) Elytron blue, legs red to blue; pronotal base punctate . . . . . *Platynus megalops* (Bates).
- 16' Elytron and legs black; pronotal base of most specimens impunctate; posterior pronotal seta present or absent . . . . . *Platynus femoralis* (Chaudoir).
- 17 (8') Basal pronotal impression distinctly punctate; [elytral intervals five and seven not setose, interval three trisetose, all intervals flat, microsculpture granulose]; [elytron aeneous or olivaceous] . . . . . *Platynus aphaedrus* (Chaudoir).
- 17' Basal pronotal impression not distinctly punctate . . . . . 18
- 18 (17'') Pronotal hind angle well developed, pronotal base straight laterally; elytral microsculpture sex-dimorphic, flat and metallic in male, granulose and opaque in female; female with more than two pairs of anal setae or not . . . . . *Platynus conicicollis* (Chaudoir).
- 18' Pronotal hind angle obsolete or nearly so, pronotal base rounded laterally . . 19
- 19 (18'') Elytral microsculpture strongly stretched. . . . . 20
- 19' Elytral microsculpture more or less isodiametric; [elytron concolorous with head and pronotum; article five of hind tarsus without distinct ventral setae]. . . 24
- 20 (19) Lateral pronotal margin plurisetose. . . . . *Platynus tenuicornis* (Chaudoir).
- 20' Lateral pronotal margin bisetose. . . . . 21
- 21 (20') Pronotum not explanate between marginal bead and discal convexity; elytral striae fine; elytra brilliant blue . . . . . *Platynus lucilius* (Bates).
- 21' Pronotum more or less explanate between marginal bead and discal convexity; elytral striae deep . . . . . 22
- 22 (21'') Elytron metallic blue . . . . . *Platynus caeruleus* (Chaudoir).
- 22' Elytron metallic green to purple, not blue . . . . . 23
- 23 (22'') Lateral pronotal margin not sinuate before hind angle . . . . . *Platynus cycloderus* (Chaudoir).
- 23' Lateral pronotal margin sinuate before hind angle . . . . . *Platynus columbinus* (Chaudoir).
- 24 (19'') Elytron bluish or purplish . . . . . *Platynus rufiventris* (Van Dyke).
- 24' Elytron piceous; [pronotum not orbate]; [alate, metepisternum elongate]; [scutellar interval pale]; [mesepisternum impunctate] . . . . . 25
- 25 (24') Pronotum more rounded, lateral explanation narrower; humeral angle of elytron more obtuse; hind femur without dorsoapical setae. . . . . *Platynus porrectus* (Chaudoir).
- 25' Pronotum more elongate, lateral explanation broader; humeral angle of elytron quite sharp, less than 120°; hind femur without (Hidalgo, Tamaulipas) or with (Jalisco, Mexico, Michoacan) dorsoapical setae . . . . . *Platynus convexulus* (Casey).
- 26 (6') Basal tarsal articles keeled; hind tarsal article four asymmetric; hind femur without dorsoapical setae; elytral microsculpture stretched; America north of Mexico (*Platynus tenuicollis* group, = *P.decentis* group in part) . . . . . *Platynus tenuicollis* LeConte).

- 26' Combination of characters not as above . . . . . 27
- 27 (26') Hind femur with one or more dorsoapical or posterior subapical setae, plus two or more posterior ventral setae (this characteristic is not reliable for all individuals of some species; some other species are keyed through both alternatives) . . . . . 28
- 27' Hind femur with two or three posterior ventral setae only, no dorsoapical setae . . . . . 58
- 28 (27) Metepisternum short; body deplanate; appendages markedly elongate; tarsi strigose above or not, with or without deep median groove; article four of front tarsus emarginate; elytron not metallic . . . . . 29
- 28' Metepisternum elongate, OR appendages not markedly elongate; body moderately to strongly convex; tarsi neither strigose not with median groove . . . . . 34
- 29 (28) Pronotal base not emarginate or trisinate; mental tooth simple (*Platynus hypolithos* group, excluding *P. ovipennis* group) . . . . . see Lindroth, 1966
- 29' Pronotal base emarginate or trisinate; mental tooth simple or bifid (*Platynus larvalis* group) . . . . . 30
- 30 (29') Species from America north of Mexico (numerous epigeal and cavernicolous species, under study by T. C. Barr) . . . . . see Lindroth, 1966
- 30' Species from Mexico . . . . . 31
- 31 (30) Cavernicolous species (named cavernicolous forms in Mexico are *Platynus arazai* (Bolivar), *P. boneti* (Bolivar and Hendrichs), *P. medellini* (Bolivar and Hendrichs), *P. pelaezi* (Bolivar and Hendrichs), and *P. rogeri* (Bolivar and Hendrichs); not further treated here . . . . . see Bolívar and Hendrichs, 1964
- 31' Epigeal species . . . . . 32
- 32 (31') Distal 1/3 to 1/2 of antennal article three pubescent . . . . . 33
- 32' Distal part of antennal article three without or with sparse pubescence; [elytral humerus strongly rounded, prominent; elytral apex produced, strongly sinuate; article five of hind tarsus strongly strigose above, article four without well defined median sulcus; lateral pronotal margin not or weakly sinuate near base, hind angle rounded to weakly angulate]. . . . . *Platynus (Rhadine) euprepes* Bates.
- 33 (32) Hind tarsus with articles four and five strigulose on dorsal surfaces; Durango, . . . . . *Platynus (Rhadine) leptodes* Bates
- 33' Hind tarsus with dorsal surfaces of articles four and five not strigulose, each with median sulcus; [elytral apex not or barely angulate; rufous, posterior 2/3 of elytral disc with piceous infuscation; Chihuahua] . . . . . *Platynus (Rhadine) perlevis* (Casey).
- 34 (28') Elytral interval three without discal setae . . . . . 35
- 34' Elytral interval three with at least one discal seta; [lateral pronotal margin with one or two setae] . . . . . 36
- 35 (34) Lateral pronotal margin plurisetose . . . . . *Platynus stricticollis* (Bates)
- 35' Lateral pronotal margin with one anterior seta only . . . . . *Platynus longipes* (Chaudoir)
- 36 (34') Elytral microsculpture strongly stretched, of dense transverse lines or at least elongate meshes; not north of Mexico; [length over 7 mm] . . . . . 37
- 36' Elytral microsculpture not strongly stretched, meshes distinct, OR north of Mexico . . . . . 42
- 37 (36) Elytron brilliant cupreous, head and pronotum metallic green; hind femur with numerous dorsoapical setae . . . . . *Platynus columbinus* (Chaudoir)
- 37' Elytron submetallic or piceous; hind femur with one to three dorsoapical setae . . . . . 38

- 38 (37') Elytron piceous, not submetallic . . . . . 39
- 38' Elytron submetallic greenish . . . . . 41
- 39 (38) Legs rufous; body broad . . . . . *Platynus platysmoides* (Bates)
- 39' Legs piceous; body narrower . . . . . 40
- 40 (39') Antenna rufous . . . . . *Platynus marginicollis* (Chaudoir)
- 40' Antenna piceous . . . . . *Platynus nyctimus* (Bates)
- 41 (38') Palpi testaceous; pronotum broad; elytral humerus oblique, basal carina regular and joined to lateral carina at sharp angle; brachypterous, metepisternum short. [pronotal hind angle acute]. . . . . *Platynus pterostichoides* (Bates)
- 41' Palpi dark; pronotum narrow; elytral humerus broadly rounded, basal carina scalloped and not joined to lateral carina at sharp angle; alate, metepisternum elongate . . . . . *Platynus brullei* (Chaudoir)
- 42 (36') Head and pronotum blue, green, or purple; pronotal hind angle obsolete; [lateral pronotal margin with one basal seta only] . . . . . 43
- 42' Head and pronotum not metallic, OR pronotal hind angle well developed; [interval three with three or four setae]; [posterolateral pronotal impression impunctate, OR elytron not blue] . . . . . 44
- 43 (42) Pronotum broad, length/width 0.90 or less . . . . . *Platynus segregatus* (Bates)
- 43' Pronotum narrower, length/width over 0.90 . . . . . *Platynus falli* (Darlington)
- 44 (42') Pronotal hind angle well developed, OR elytral microsculpture stretched, OR frons with two rufous spots . . . . . 45
- 44' Pronotal hind angle obsolete or nearly so, OR, if distinct but obtuse then elytral apex bidenticulate and body pale; elytral microsculpture isodiametric or nearly so; frons without rufous spots . . . . . 52
- 45 (44) Lateral pronotal margin with one seta, OR pronotum not concolorous with submetallic elytron . . . . . 46
- 45' Lateral pronotal margin with two setae, and elytron concolorous with head and pronotum . . . . . 47
- 46 (45) Lateral pronotal margin with anterior seta only . . . . . *Platynus transfuga* (Chaudoir)
- 46' Lateral pronotal margin with two setae; [elytron submetallic, head and pronotum black] . . . . . *Platynus harpaloides* (Bates)
- 47 (45') North of Mexico (*Platynus decentis* group, excluding *P. tenuicollis* and *P. trifoveolatus* groups) . . . . . see Lindroth, 1966
- 47' Mexico; [if elytral microsculpture stretched, then elytral apex rounded, not denticulate]. . . . . 48
- 48 (47) Pronotum narrow, length/width over 0.85, lateral explanation reflexed, base straight laterally in most specimens; elytral microsculpture stretched or not . . . . . 49
- 48' Pronotum broad, length/width under 0.85, lateral explanation narrow, base rounded or oblique laterally; elytral microsculpture not stretched . . . . . 50
- 49 (48) Elytron opaque from granulose microsculpture; basal pronotal margin interrupted medially . . . . . *Platynus logicus* (Casey)
- 49' Elytron less opaque, microsculpture flatter, stretched in some specimens; basal pronotal margin continuous medially . . . . . *Platynus nitidus* (Chaudoir)
- 50 (48') Elytral microsculpture subgranulose, neither much flattened nor strongly granulose; posterolateral pronotal impression broad, no strong convexity between side margin and impression; black to slightly purplish to metallic green or purple . . . . . *Platynus monachus* (Dejean)

- 50' Combination of characters not as above; [elytron opaque to shiny, striae shallow, intervals flat; length under 12 mm] . . . . . 51
- 51 (50') Head large; elytron shiny; pronotum about as wide between front angles as between hind angles. . . . . *Platynus lugens* (Dejean)
- 51' Head small; elytron opaque; pronotal width between front angles no more than 0.90 width between hind angles . . . . . *Platynus moestus* (Dejean)
- 52 (44') Metepisternum short, nearly square . . . . . 53
- 52' Metepisternum more elongated . . . . . 55
- 53 (52) Posterior pronotal seta distant from margin, no trace of hind angle; [length over 10 mm; rufotestaceous to purplish or greenish black] . . . . . 54
- 53' Posterior pronotal seta on margin, hind angle obsolete to obtuse; [elytron purplish, not or moderately dull and opaque, striae deep] . *Platynus valens* (Bates)
- 54 (53) Pronotum elongate; hind femur with numerous dorsoapical setae . . . . .  
. . . . . *Platynus chihuahuae* Bates
- 54' Pronotum broad . . . . . *Platynus durangensis* (Bates)
- 55 (52') Lateral pronotal margin with one seta, at hind angle. . . . .  
. . . . . *Platynus (Stenoplatynus) umbripennis* (Casey)
- 55' Lateral pronotal margin with two setae . . . . . 56
- 56 (55') Lateral pronotal margin not markedly sinuate; [mesepisternum impunctate; length under 7 mm; brachypterous, metepisternum shortened; elytron not piceous, not aeneous]. . . . . *Platynus minimus* (Bates)
- 56' Lateral pronotal margin sinuate, OR mesepisternum and metepisternum impunctate and length over 11 mm. . . . . 57
- 57 (56') Length over 11 mm; dorsoapical setae of hind femur much shorter than tibial setae . . . . . *Platynus forreri* (Bates)
- 57' Length under 11 mm; dorsoapical setae of hind femur about as long as tibial setae; [elytral striae strongly punctate; elytral microsculpture somewhat stretched] . . . . . *Platynus deyrollei* (Chaudoir)
- 58 (27') Head with basal supraorbital seta only; lateral pronotal margin with anterior seta only. . . . . 59
- 58' Head with two supraorbital setae on each side . . . . . 62
- 59 (58) Pronotal hind angle completely rounded; elytra fused, apices not or barely sinuate . . . . . *Platynus steropoides* (Bates)
- 59' Pronotal hind angle well developed; elytra not fused, apices clearly sinuate . . 60
- 60 (59') Large, over 12 mm; opaque, elytral intervals flat, microsculpture strongly granulose . . . . . *Platynus sphodroides* (Chaudoir)
- 60' Small, under 12 mm; more shiny, elytron more ovate, intervals slightly convex microsculpture more flattened . . . . . 61
- 61 (60') Elytral microsculpture strongly raised; pronotum strongly constricted at base, lateral margin strongly sinuate . . . . . *Platynus pristonychoides* (Chaudoir)
- 61' Elytral microsculpture quite flat; pronotum not strongly constricted at base, lateral margin weakly sinuate . . . *Platynus (Anacolpodes) rectilineus* (Bates)
- 62 (58') Lateral pronotal margin with anterior seta only; [brachypterous, metepisternum short; elytral striae distinct] . . . . . 63
- 62' Lateral pronotal margin with one or two setae, posterior seta present . . . 68
- 63 (10, 62) Elytral microsculpture strongly stretched; elytron shiny, submetallic; [pronotal hind angle completely obsolete]. . . . . *Platynus championi* (Bates)
- 63' Elytral microsculpture not or slightly stretched; black or submetallic . . . 64



- 64 (63') Pronotal hind angle prominent . . . . . 65
- 64' Pronotal hind angle obsolete or nearly so, lateral pronotal margin not or hardly sinuate . . . . . 66
- 65 (64) Pronotal hind angle nearly right, abruptly rounded at tip . . . . .  
. . . . . *Platynus baroni* (Casey)
- 65' Pronotal hind angle more obtuse. . . . . *Platynus transfuga* (Chaudoir)
- 66 (64') Elytron submetallic. . . . . *Platynus procephalus* (Bates)
- 66' Elytron piceous or black. . . . . 67
- 67 (66') Pronotal base broadly rounded laterally, hind angle obsolete; elytral humerus prominent, basal and lateral carinae joined at nearly right angle . . . . .  
. . . . . *Platynus semiopacus* (Chaudoir)
- 67' Pronotal base nearly straight laterally, rounded rather abruptly into lateral margin; elytral humerus less prominent, basal and lateral carinae joined at obtuse angle . . . . . *Platynus biovatus* (Chaudoir)
- 68 (62') Pronotum with posterior seta only; [alate, metepisternum elongate; elytron blue or green] . . . . . 69
- 68' Pronotum with anterior and posterior setae . . . . . 74
- 69 (68) Pronotum blue or blue-green, concolorous with elytron . . . . .  
. . . . . *Platynus cyanides* (Bates)
- 69' Pronotum castaneous to piceous, elytron metallic green; [elytral apex rounded] . . . . . 70
- 70 (69') Pronotum widest at extreme base; female with median anal setae distant from margin . . . . . 71
- 70' Pronotum widest in front of base, near middle; female with median anal setae near margin . . . . . 72
- 71 (70) Elytral striae deep, indistinctly punctate; elytral apex rounded, not cupreous . . . . .  
. . . . . *Platynus quadrilaterus* (Bates)
- 71' Elytral striae shallow, distinctly punctate; elytral apex in most specimens angulate, cupreous . . . . . *Platynus iricolor* (Bates)
- 72 (70') Elytral striae strongly punctate; pronotal base in most specimens conspicuously punctate; lateral pronotal explanation broad; length under 10 mm . . . . .  
. . . . . *Platynus orbicollis* (Chaudoir)
- 72' Elytral striae finely punctate; pronotal base impunctate or nearly so . . . . . 73
- 73 (72') Length over 10 mm; lateral pronotal explanation broad . . . . .  
. . . . . *Platynus phaeolomus* (Chaudoir)
- 73' Length under 10 mm; lateral pronotal explanation narrow . . . . .  
. . . . . *Platynus erythrocerus* (Chaudoir)
- 74 (68') Elytral apex strongly acuminate, inner edge concave . . . . .  
. . . . . *Platynus spinifer* (Bates)
- 74' Elytral apex at most acute, inner edge not concave. . . . . 75
- 75 (74') Elytral microsculpture isodiametric or nearly so AND/OR pronotum essentially trapezoidal; length over 7 mm AND/OR posterior pronotal seta remote from margin (some specimens of *P. severus* and *P. teter*, large black species from Chiapas, have quite stretched microsculpture) . . . . . 76
- 75' Elytral microsculpture definitely stretched OR length under 7 mm and posterior pronotal seta on or near margin; pronotum not trapezoidal; [without following combination of characters: length over 10 mm, body blue; pronotal hind angle rounded, posterolateral impression punctate; elytral striae deep, not coarsely punctate basally]. . . . . 87

- 76 (75) Prosternal apex more or less distinctly truncate; metepisternum about two times as long as wide; brachypterous; rufotestaceous . . . . . *Platynus (Mexisphodrus) veraecrucis* (Barr)
- 76' Prosternal apex not truncate, or other characters not as above; [pronotal disc without distinct microsculpture AND/OR lateral pronotal explanation narrow] . . . . . 77
- 77 (76') Posterior pronotal seta in most species remote from margin; metepisternum elongate; lateral pronotal explanation wide and translucent, margin not or barely sinuate; pronotum nearly as wide at base as at middle, more or less trapezoidal . . . . . 78
- 77' Posterior pronotal seta on or near margin OR metepisternum short; pronotum constricted near base, not trapezoidal . . . . . 80
- 78 (77) Pronotal front angle strongly produced; [elytral microsculpture isodiametric, in male flattened and shining]. . . . . *Platynus conicicollis* (Chaudoir)
- 78' Pronotal front angle not or slightly produced; [lateral pronotal explanation narrowed in front; elytral microsculpture not sex-dimorphic] . . . . . 79
- 79 (78') Elytral microsculpture stretched . . . . . *Platynus inops* (Chaudoir)
- 79' Elytral microsculpture isodiametric; [palpi in most specimens pale; length over 10 mm] . . . . . *Platynus (Trapezodera) aeneicauda* (Bates)
- 80 (77') Bright blue, green, or purple; wing-dimorphic . . . . . *Platynus monachus* (Dejean)
- 80' Testaceous to piceous, at most slightly aeneous; [legs dark, concolorous with body, or elytron not strongly alutaceous] . . . . . 81
- 81 (80') Elytron dull from granulose microsculpture; pronotal base straight or nearly so laterally . . . . . *Platynus logicus* (Casey)
- 81' Elytron quite shiny, or pronotal base strongly oblique or rounded laterally; [posterior pronotal seta on or near margin] . . . . . 82
- 82 (81') Metepisternum elongate; [lateral pronotal explanation narrow; elytron bluish, shining] . . . . . *Platynus porrectus* (Chaudoir)
- 82' Brachypterous, metepisternum no more than twice as long as wide; elytron not aeneous . . . . . 83
- 83 (82') Elytron distinctly bluish or purplish; lateral pronotal explanation narrow . . . . . *Platynus monachus* (Dejean).
- 83' Elytron not bluish or purplish; lateral pronotal explanation various . . . . . 84
- 84 (83') Narrower, pronotal length/width over 0.85; lateral pronotal explanation relatively narrow; [pronotal hind angle distinct, in most specimens sharp] . . . . . *Platynus nitidus* (Chaudoir)
- 84' Broader, pronotal length/width under 0.85; lateral pronotal explanation in most species wider; [pronotal base rounded or oblique laterally] . . . . . 85
- 85 (84') Lateral pronotal explanation narrow; [pronotal hind angle right; length 11-12 mm] . . . . . *Platynus tinctipennis* (Bates)
- 85' Lateral pronotal explanation broad; [elytral humerus not strongly produced, epipleural and basal carinae joined at obtuse angle] . . . . . 86
- 86 (85') Pronotal hind angle narrowly rounded, more or less evident; pronotum more cordate, lateral margin more distinctly sinuate and explanation less strongly reflexed . . . . . *Platynus teter* (Chaudoir)
- 86' Pronotal hind angle broadly rounded, obsolete; pronotum less cordate, lateral margin not sinuate, explanation strongly reflexed. . . . . *Platynus severus* (Chaudoir)

- 87 (75') Elytron blue, head and pronotum red; posterolateral pronotal impression punctate; lateral pronotal margin sinuate, hind angle evident . . . . . *Platynus colibor* Whitehead
- 87' Not so colored, OR otherwise not as above . . . . . 88
- 88 (87') Length under 7 mm; mental tooth simple, acute; pronotum broadly rounded, lateral explanation broad, lateral margin not or barely sinuate; pronotal hind angle obsolete or nearly so, denticulate in some species; elytral striae moderately to deeply engraved; [intercoxal process of prosternum not lipped at apex, not sharply truncate; eye normal, lateral frontal sulcus neither much deepened nor extended far beyond eye; metepisternum elongate] . . . . . 89
- 88' Combination of characters not as above . . . . . 90
- 89 (88) Pronotal base straight laterally, hind angle evident though obtuse; elytral microsculpture of dense transverse lines; [piceous, elytral striae deep] . . . . . *Platynus dominicensis* (Bates)
- 89' Pronotal base rounded laterally, hind angle obsolete or nearly so; [elytral microsculpture of slightly stretched meshes; dark brown, shiny, not or slightly aeneous] . . . . . *Platynus ovatulus* (Bates)
- 90 (88') Article four of hind tarsus with outer lobe at least twice as long as inner lobe and longer than base . . . . . 91
- 90' Article four of hind tarsus with outer lobe less than twice as long as inner lobe, shorter than base or not . . . . . 99
- 91 (90) Legs, including femora, rufous or slightly infuscated; [elytron metallic green, head and pronotum reddish or slightly infuscated; mental tooth acute] . . . . . *Platynus scabricollis* (Bates)
- 91' Legs, including femora, strongly infuscated; mental tooth narrow, rounded or acute . . . . . 92
- 92 (91') Piceous; elytral striae coarsely punctate basally; [elytral striae shallowly engraved basally] . . . . . 93
- 92' Submetallic to metallic blue, green, or cupreous . . . . . 94
- 93 (92) Elytral microsculpture more open, of more or less distinct though strongly stretched meshes. . . . . *Platynus niger* (Chaudoir)
- 93' Elytral microsculpture of dense transverse lines, indistinct at lower magnifications; pronotum broader . . . . . *Platynus picicornis* (Chaudoir)
- 94 (92') Elytral striae fine to obsolete, interrupted throughout . . . . . 95
- 94' Elytral striae, at least toward apex, uninterrupted; [basal antennal articles pale, AND/OR posterolateral pronotal impression not densely punctate] . . . . . 96
- 95 (94) Elytron metallic green; elytral striae more distinct . . . . . *Platynus metallicus* (Chaudoir)
- 95' Elytron metallic cupreous; elytral striae indistinct, reduced to fine punctures . . . . . *Platynus chaudoiri* (Coquerel)
- 96 (94') Elytral striae neither coarsely punctate nor interrupted basally; [pronotal base not oblique or rounded laterally, OR basal bead of pronotum not extended nearly to hind angle, OR elytron not greenish or blue, OR elytral microsculpture not of distinct meshes, OR lateral pronotal explanation broad and translucent in front, OR posterolateral pronotal impression not both densely punctate and coarsely microsculptured] . . . . . 97

- 96' Elytral striae either coarsely punctate or interrupted basally; head and pronotum metallic, elytron metallic green; [elytral striae coarsely punctate basally, uninterrupted; lateral pronotal explanation narrowed in front, front angle not produced] . . . . . *Platynus ruficornis* (Chaudoir)
- 97 (96) Elytral microsculpture of dense transverse lines . . . . . *Platynus transversicollis* (Chaudoir)
- 97' Elytral microsculpture more open, meshes more or less distinct . . . . . 98
- 98 (97') Elytron submetallic, cupreous . . . . . *Platynus reflexus* (Chaudoir)
- 98' Elytron not strongly cupreous . . . . . *Platynus fratellus* (Chaudoir)
- 99 (90') Elytral striae coarsely punctate basally; [elytral microsculpture of dense transverse lines; alate; metepisternum elongate] . . . . . *Platynus striatopunctatus* (Chaudoir)
- 99' Elytral striae finely to indistinctly punctate basally . . . . . 100
- 100 (99') Brachypterous; metepisternum short, less than twice as long as wide, OR, if alate then legs clearly paler than rest of body; most species unmetallic, some species faintly submetallic or violaceous . . . . . 101
- 100' Metepisternum elongate, most specimens alate; elytron in most species at least submetallic, in some strongly metallic; legs not strikingly paler than body except in *P. pectoralis* with strongly submetallic elytron . . . . . 119
- 101 (100) Elytral interval three with one apical seta only . . . . . 102
- 101' Elytral interval three with two or three setae . . . . . 103
- 102 (101) Elytron violet; outer striae obsolete near humerus . . . . . *Platynus lyrophorus* (Chaudoir)
- 102' Elytron piceous, unmetallic; outer striae reduced but distinct near humerus . . . . . *Platynus amplicollis* (Chaudoir)
- 103 (101') Elytron bright violet, metallic; lateral pronotal margin strongly sinuate; mental tooth narrow, acute . . . . . *Platynus cupripennis* (Laporte)
- 103' Combination not as above; elytron purplish or not, but not bright violet; [basal and outer antennal articles not sharply contrasted in color]; [combination not as follows: pronotal hind angle obsolete, explanation narrow, lateral margin sinuate, basal bead continuous to side; brown, legs reddish] . . . . . 104
- 104 (103') Basal carina of elytron strongly sinuate and in most specimens irregular, inner portion deeply emarginate; black, shining; elytral microsculpture of dense, transverse lines; elytral striae distinctly punctate basally; length under 10 mm . . . . . *Platynus purulensis* (Bates)
- 104' Combination of characters not as above . . . . . 105
- 105 (104') Mental tooth narrow at apex, rounded or acute . . . . . 106
- 105' Mental tooth broad at apex, truncate or bifid . . . . . 110
- 106 (105) Pronotal base straight or nearly so laterally, hind angle sharply developed . 107
- 106' Pronotal base rounded or oblique laterally, hind angle rounded to obtuse; [basal and epipleural carinae joined at obtuse angle; elytron strongly submetallic, not iridescent; length over 7 mm] . . . *Platynus macrous* (Chaudoir)
- 107 (106) Elytra fused . . . . . *Platynus robustus* (Chaudoir)
- 107' Elytra not fused; [pronotum not strongly cordate; if pronotal hind angle right then elytral microsculpture of distinct meshes] . . . . . 108
- 108 (107') Elytron more or less iridescent, or with faint but distinct bronze or purplish luster; lateral pronotal margin weakly sinuate, hind angle denticulate; elytral microsculpture tending to form dense transverse lines; pronotum relatively strong-

ly cordate; [elytral apex more or less truncate, sutural angle more or less denticulate; body pale rufous, elytron more or less infuscated] . . . . .

. . . . . *Platynus tlamayensis* (Barr)

108' Elytron without submetallic luster, microsculpture tending to form distinct meshes. . . . . 109

109 (108') Article four of hind tarsus with outer lobe about as long as base; [elytron testaceous; eye reduced]. . . . . *Platynus profundus* (Barr)

109' Article four of hind tarsus with outer lobe only slightly longer than inner lobe and much less than half length of base . . . . . *Platynus nitidus* (Chaudoir)

110 (105') Outer elytral striae much less deeply engraved than inner striae, or obsolete. 111

110' Outer elytral striae as deeply engraved as inner striae; [elytron definitely sinuate behind, OR interval three with three setae, OR pronotal hind angle obtuse, neither prominent nor completely rounded]; [not combination of: large, black; pronotum convex, lateral explanation narrow, basal bead continuous to side, hind angle distinct]. . . . . 112

111 (110) Basal elytral carina strongly arcuate, lateral carina broadly rounded at humerus; color iridescent, not purplish; antenna pale . . . . .

. . . . . *Platynus ebeninus* (Chaudoir)

111' Basal elytral carina normal, joined to lateral carina at humerus; color purplish, not iridescent; antenna dark . . . . . *Platynus consularis* (Casey)

112 (110') Body broad; [pronotal base straight or curved backward laterally; basal puncture of elytral interval three not foveate]. . . . . 113

112' Body narrow . . . . . 114

113 (112) Elytron cupreous, microsculpture fine and dense . . . . . *Platynus pterostichoides* (Bates)

113' Elytron piceous, microsculpture stronger and coarser . . . . . *Platynus haptoderoides* (Bates)

114 (112') Elytron with distinct bluish or greenish sheen, microsculpture of quite dense lines or strongly stretched meshes OR posterolateral pronotal impression punctate; length 7 mm or more . . . . . 115

114' Elytron brownish to nearly black, at most with faint bluish luster; microsculpture tending to form distinct meshes, or length under 7 mm . . . . . 116

115 (114) Legs more or less infuscated; pronotal hind angle about right in most specimens . . . . . *Platynus obscurus* (Chaudoir)

115' Legs pale; [pronotal base oblique laterally, hind angle obtuse and/or basal impression punctate] . . . . . *Platynus lyratus* (Chaudoir)

116 (114') Article four of hind tarsus deeply lobate; north of Mexico (Appalachians) (*P. trifoveolatus* group, = *P. decentis* group in part, includes only *P. trifoveolatus* Beutenmüller) . . . . . see Lindroth, 1966

116' Article four of hind tarsus shallowly emarginate or shallowly lobate; Mexico . . . . . 117

117 (116') Pronotal base straight laterally, hind angle acute: [length under 7 mm] . . . . . *Platynus angulosus* (Chaudoir)

117' Pronotal base oblique laterally, hind angle right to obtuse . . . . . 118

118 (117') Pronotal base broad, posterolateral impression in most specimens strongly tuberculate; length under 7 mm; [pronotal hind angle about right, lateral pronotal margin strongly sinuate, explanation more or less reflexed] . . . . .

. . . . . *Platynus nugax* (Bates)

- 118' Pronotal base narrower, posterolateral impression in most specimens not tuberculate; [length under 7 mm OR elytral microsculpture of evident meshes; pronotal base in most specimens narrow] . . . . . *Platynus concisus* (Bates)
- 119 (100') Lateral pronotal margin grossly reflexed; elytron strongly striate, cupreous . . . . . *Platynus reflexicollis* (Chaudoir)
- 119' Lateral pronotal margin at most moderately reflexed . . . . . 120
- 120 (119') Pronotum cordate, lateral margin distinctly sinuate; first article of hind tarsus clearly bisulcate; mental tooth narrow, rounded or acute; legs infuscated; elytron with faint to strong purplish luster or metallic; posterolateral pronotal impression not or sparsely punctate . . . . . 121
- 120' Combination of characters not as above. . . . . 127
- 121 (120) Elytral apex sharp; [elytron metallic greenish or violaceous] . . . . . *Platynus cordatus* (Chaudoir)
- 121' Elytral apex rounded . . . . . 122
- 122 (121') Elytron bright metallic green, coppery, or violet . . . . . 123
- 122' Elytron bright blue or submetallic purplish or greenish; [pronotum about as wide at apex as at base] . . . . . 125
- 123 (122) Palpi pale; [elytral striae deep, intervals convex] . . . . . *Platynus validus* (Chaudoir)
- 123' Palpi infuscated . . . . . 124
- 124 (123') Elytral striae two to eight shallow, contrasted with deep sutural stria . . . . . *Platynus purpuratus* (Reiche)
- 124' Elytral striae uniformly deep; pronotal form varied . . . . . *Platynus variabilis* (Chaudoir)
- 125 (122'') Metepisternum shorter; piceous, only slightly purple . . . . . *Platynus violaceipennis* (Chaudoir)
- 125' Metepisternum more elongate; alate or wing-dimorphic; most specimens more brightly colored . . . . . 126
- 126 (125'') Elytron bright blue . . . . . *Platynus aequinoctialis* (Chaudoir)
- 126' Elytron violaceous or greenish, violet-blue in some specimens . . . . . *Platynus subcyaneus* (Chaudoir)
- 127 (120'') Article five of hind tarsus conspicuously ciliate beneath AND/OR elytral punctures strongly foveate . . . . . 128
- 127' Article five of hind tarsus not conspicuously ciliate beneath; elytral punctures not foveate . . . . . 129
- 128 (127) Black, non-metallic . . . . . *Platynus obscurellus* (Bates)
- 128' Metallic . . . . . *Platynus sexfoveolatus* (Chaudoir)
- 129 (127'') Elytron deep blue; [posterolateral pronotal impression punctate; palpi pale] . . . . . *Platynus obscurus* (Chaudoir)
- 129' Elytron not deep blue; [elytron unicolorous] . . . . . 130
- 130 (129'') Elytron bright green; posterolateral pronotal impression coarsely and densely punctate; [pronotal hind angle sharp, nearly right] . . . . . *Platynus limbicollis* (Chaudoir)
- 130' Combination of characters not as above; [body narrow; OR pronotal base not straight laterally, hind angle not acute; OR pronotum not strongly narrowed behind; OR elytron not piceous]; [elytron at least submetallic, if not distinctly so then length over 8 mm]; [elytral microsculpture strongly stretched] . . 131

- 131 (130') Antenna and palpi dark; lateral pronotal margin strongly sinuate; [ head and pronotum metallic; elytron metallic green, margin in most specimens metallic blue]. . . . . *Platynus caeruleomarginatus* (Mannerheim)
- 131' Antenna and palpi pale to reddish OR lateral pronotal margin not strongly sinuate; [pronotum narrow, OR lateral pronotal explanation punctate]; [elytral striae well engraved throughout, shallow to deep] . . . . . 132
- 132 (131') Frons and pronotal disc with distinct microsculpture . . . . . 133
- 132' Frons without distinct microsculpture between eyes . . . . . 137
- 133 (132) Elytral microsculpture more open, of more or less distinct though strongly stretched meshes . . . . . 134
- 133' Elytral microsculpture of dense transverse lines, no evident meshes; [lateral pronotal margin sinuate or not, lateral explanation narrow] . . . . . 135
- 134 (133) Length under 10 mm; head and pronotum pale . *Platynus subauratus* (Bates)
- 134' Length over 10 mm; head and pronotum dark; [pronotum narrow, length/width over 0.80; posterolateral impression not tuberculate]; [lateral pronotal explanation narrow] . . . . . *Platynus gracilis* (Chaudoir)
- 135 (133') Length about 10 mm; elytron rufopiceous, unmetallic, with slight bluish luster; legs pale; pronotal hind angle sharp, about 100°. . . . .  
. . . . . *Platynus brachyderus* (Chaudoir)
- 135' Combination of characters not as above . . . . . 136
- 136 (135') Length about 8 mm; elytron metallic green; pronotal hind angle distinct; legs pale . . . . . *Platynus dilutus* (Chaudoir)
- 136' Length about 10 mm; pronotal hind angle rounded, indistinct; [legs pale; elytron at most submetallic, striae shallow; according to original description, sternum black with abdomen pale] . . . . . *Platynus pectoralis* (Chaudoir)
- 137 (132) Elytral microsculpture of more or less distinct meshes . . . . . 138
- 137' Elytral microsculpture dense, not of distinct meshes . . . . . 139
- 138 (137) Pronotal hind angle quite obtuse, over 100° . . *Platynus olivaceus* (Chaudoir)
- 138' Pronotal hind angle sharp, nearly right . . . . *Platynus rubidus* (Chaudoir)
- 139 (137') Head and pronotum pale to lightly infusate . . . . . 140
- 139' Head and in most specimens pronotum quite dark, in most specimens piceous . . . . . 141
- 140 (139) Pronotal front angle produced, hind angle sharp . *Platynus ilagis* Whitehead
- 140' Pronotal front angle not produced, OR hind angle obtuse; [lateral pronotal explanation moderately narrow] . . . . . *Platynus laetiusculus* (Chaudoir)
- 141 (139') Pronotal hind angle sharp, nearly right, lateral pronotal margin quite sinuate . . . . . *Platynus acutulus* (Bates)
- 141' Pronotal hind angle quite obtuse, blunt, over 100°, lateral pronotal margin less sinuate; [article four of hind tarsus not strongly lobate, hardly more than emarginate; article one of front tarsus not or weakly bisulcate]; [lateral pronotal margin clearly sinuate, hind angle well developed]; [length of most specimens over 8.5 mm; pronotum elongate, length/width over 0.80 in most specimens] . . . . . *Platynus lifragis* Whitehead

# ANNOTATED LIST OF SPECIES

*Platynus acuminatus* (Chevrolat), new combination.

*Dyscolus acuminatus* Chevrolat 1835: no. 185. Lectotype female, here designated, selected by G. E. Ball, "Stenocranius acuminatus Chev. Dyscolus ch6 1837 pro. Mex" (Hope Mu-

seum, Oxford). Type locality "Mexique", here restricted to Cordova, Veracruz, Mexico.

*Stenocnemus chevrolati* Chaudoir 1837:10. Lectotype male, here designated, "Stenocnemus chevrolatii Chd." and "Ex Musaeo Chaudoir" (MNHP, 295/5/2). Type locality "Mexique", subsequently restricted by Chaudoir (1859) to "Cordova", Veracruz, Mexico.

*Colpodes acuminatus*, Chaudoir 1859:339 (subgenus *Stenocnemus*); Chaudoir 1878:335; Bates 1882:115; Csiki 1931:746; Blackwelder 1944:37.

This distinctive species, one of several that may be assigned to the subgenus *Stenocnemus*, ranges in Mexico from Nuevo Leon and Sinaloa south to Veracruz and Oaxaca, at low elevations.

*Platynus acutulus* (Bates), new combination.

*Colpodes acutulus* Bates 1891:259. Lectotype male, here designated, "Zacualtipan Hidalgo Höge" and "Sp. figured" (BMNH).

*Colpodes acutulus*, Csiki 1931:746; Blackwelder 1944:37.

This wide-ranging species, which occurs in Mexico from San Luis Potosi to Chiapas, is a member of a complex which needs revision.

*Platynus (Trapezodera) aeneicauda* (Bates), new combination.

*Colpodes aeneicauda* Bates 1891:259. Lectotype male, here designated, "TYPE H.T.", "Xucumanatlan, Guerrero 7000 ft. July H.H. Smith", "Colpodes aeneicauda, Bates 1891-64" (BMNH).

*Colpodes aeneicauda*, Csiki 1931:746; Blackwelder 1944:37.

*Trapezodera aeneicauda*, Casey 1920:19.

This species is related to *P. inops* and some undescribed species, and with them may be assigned to the subgenus *Trapezodera*. I have examined specimens of this species from the Mexican states of Guerrero, Mexico, and Morelos.

*Platynus aequinoctialis* (Chaudoir), new combination.

*Dyscolus (Ophryodactylus) aequinoctialis* Chaudoir 1850:382. Lectotype male, here designated, first specimen labelled "Ex Musaeo Chaudoir" (MNHP, 295/6/7); box label states "Goudot coll Laferté". A female labelled "C. aequinoctialis" and "Ex Musaeo Salle 1897" may not have been seen by Chaudoir. Type locality "Nouvelle-Grenade"; Chaudoir (1859) reported specimens sent by Sallé and Guérin from Colombia.

*Colpodes aequinoctialis*, Chaudoir 1859:339; Chaudoir 1878:339. Bates 1882:118; Csiki 1931:746; Blackwelder 1944:37.

I have examined numerous specimens from the Mexican states of Oaxaca and Veracruz, northern South America, and the West Indies. The complex to which this species belongs needs revision; other forms here recognized as distinct species may prove conspecific, notably *P. subcyaneus*.

[*Platynus agilis* (Chaudoir), see *P. ilagis* Whitehead].

*Platynus amplicollis* (Chaudoir), new combination.

*Colpodes amplicollis* Chaudoir 1878:320. Lectotype male, here designated, "6<sup>e</sup> sect.", "Ex Musaeo Chaudoir" (MNHP). Type locality "Mexique", here restricted to 13.2 mi.w. Ciudad Mendoza, Veracruz, Mexico.

*Colpodes amplicollis*, Bates 1882:110; Csiki 1931:747; Blackwelder 1944:37.

This distinctive species is related to *P. cupripennis* and *P. lyrophorus*. In addition to the



restricted type locality, *P. amplicollis* has been reported from Orizaba, Veracruz, Mexico by Bates (1882).

[*Platynus anchomenoides* (Chaudoir), see *P. lugens* (Dejean)].

*Platynus angulosus* (Chaudoir), new combination.

*Colpodes angulosus* Chaudoir 1878:299. Holotype female, "Ex Musaeo Chaudoir" (MNHP); specimen originally from Reiche collection, now in Oberthür collection. Type locality "Mexique".

*Colpodes concisus*, in part, Bates 1882:104; Csiki 1931:751; Blackwelder 1944:38.

This name may be synonymous with *P. concisus*, but I provisionally treat it as representing a distinct species. I have examined specimens from various localities in the state of Mexico.

*Platynus aphaedrus* (Chaudoir), new combination.

*Colpodes aphaedrus* Chaudoir 1859:321. Lectotype female, here designated, first specimen labelled "Ex Musaeo Chaudoir" (MNHP, 295/3/3). A male labelled "Mex", "aphaedrus Chaud. An. Soc. Ent. II. 321", and "Ex Musaeo Salle 1897" probably was not examined by Chaudoir. Three specimens were originally reported, though four are represented in authentic Chaudoir material. Type locality "Orizaba", Veracruz, Mexico.

*Colpodes aphaedrus*, Bates 1882: 112; Csiki 1931:747; Blackwelder 1944:37.

In Mexico, this species is known from the states of Chiapas, Oaxaca, and Veracruz. It is related to several undescribed species from elsewhere in Mexico and Arizona.

[*Platynus approximatus* (Chaudoir), see *P. tenuicollis* (LeConte)].

*Platynus (Rhadine) araizi* (Bolivar), new combination.

See Bolivar and Hendrichs, 1964.

[*Platynus atratus* (Chaudoir), see *P. obscurellus* (Bates)].

*Platynus baroni* (Casey), new combination.

*Anchomenus (Platynella) baroni* Casey 1920:25. Holotype female, "Guerrero", "USNM TYPE 47395" (USNM).

*Agonum baroni*, Csiki 1931:849 (subgenus *Platynella*); Blackwelder 1944:41.

*Platynus baroni* and *P. transfuga* may be conspecific allopatric forms; *P. baroni* is known only from the type specimen.

[*Platynus bicolor* (Chaudoir), see *P. colibor* Whitehead].

[*Platynus bilimeki* (Bolivar and Hendrichs), see *P. umbripennis* (Casey)].

*Platynus biovatus* (Chaudoir), new combination.

*Colpodes biovatus* Chaudoir 1878:322. Holotype female, "TYPE H.T.", "Yolotepec", "Mexico. Salle Coll.", "538" (BMNH). Type locality originally cited as "Mexique" but restricted to Yolotepec, Oaxaca, Mexico by label data on type specimen.

*Colpodes biovatus*, Bates 1882:106; Csiki 1931:748; Blackwelder 1944:38.

The complex to which *P. biovatus* and *P. semiopacus* belong needs revision; these names

may not apply to reproductive isolates. Aside from the type specimen of *P. biovatus*, specimens under that name in the Biologia collection (BMNH) and records cited by Bates (1882) evidently pertain to *P. semiopacus*. I have examined specimens from 3.4 mi. s. Suchixtepec, Oaxaca, Mexico which I think are conspecific with the type specimen of *P. biovatus* though they differ in various details.

*Platynus (Rhadine) boneti* (Bolivar and Hendrichs), new combination.

See Bolívar and Hendrichs, 1964.

*Platynus brachyderus* (Chaudoir), new combination.

*Colpodes brachyderus* Chaudoir 1878:327. Lectotype female, here designated, "Chiapas 5-7-58", "Soc. Ent. Belg. Coll. Putzeys", "C. brachyderus Chaud" (in Chaudoir script) (IRSB).

*Colpodes brachyderus*, Bates 1882:112; Csiki 1931:749; Blackwelder 1944:38.

Two additional specimens originally reported by Chaudoir were from "Toxpam", Veracruz, Mexico. A female (BMNH), reported by Bates, is labelled "Cordova", "Mexico. Salle Coll.", "543"; this may be a syntype. The Chiapas and Cordova specimens both differ from Chaudoir's original description by clearly bisulcate hind tarsal articles. I have seen further specimens of this species from various localities in Chiapas.

*Platynus brullei* (Chaudoir), new combination.

*Anchomenus brullei* Chaudoir 1837:23. Lectotype male, here designated, "Ex Musaeo Chaudoir" (MNHP, 296/2/1); two male and one female paralectotypes, same label data. A male, "Mex Brullei Chev." and "Ex Musaeo Salle 1897", is here regarded as not seen by Chaudoir, though *brullei* was a Chevrolat manuscript name, and Chaudoir had one specimen from Chevrolat which perhaps originally came from Sallé (Chaudoir, 1859). This specimen is conspecific with specimens here considered as syntypes. Type locality "Mexique".

*Colpodes brullei*, Chaudoir 1859:330; Chaudoir 1878:341; Bates 1882:119; Csiki 1931:749; Blackwelder 1944:38.

Specimens of this species are readily distinguished from all others known from Mexico. I have seen Mexican specimens from low elevations in the states of Chiapas and Veracruz.

[*Platynus brunnipennis* (Chaudoir), see *P. lugens* (Dejean)].

*Platynus caeruleomarginatus* (Mannerheim), new combination.

*Dyscolus caeruleomarginatus* Mannerheim 1837:45. Type not seen, perhaps in Helsinki. Type locality "Mexico".

*Colpodes caeruleomarginatus*, Chaudoir 1859:343; Chaudoir 1878:350; Bates 1882:123; Heyne-Taschenberg 1908:25.

*Colpodes coeruleomarginatus*, Csiki 1931:751; Blackwelder 1944:38.

As I have not seen type material of *P. caeruleomarginatus*, I accept Chaudoir's and Bates' association of the name. This species is widespread in tropical lowlands of Mexico and belongs to an otherwise Middle and South American complex that requires revision.

*Platynus caeruleus* (Chaudoir), new combination.

*Colpodes caeruleus* Chaudoir 1859:335. Lectotype male, here designated, first male labelled "Ex Musaeo Chaudoir" (MNHP 295/4/5). Chaudoir originally reported one male and one female sent by Sallé, but the Oberthür collection contains seven authentic Chaudoir specimens. Another male in the Oberthür collection, "caeruleus Chaud", "Dyscolus cyanea Chev.

in Dej. cat.", probably was not examined by Chaudoir. Type locality "Orizaba", Veracruz, Mexico.

*Colpodes caeruleus*, Chaudoir 1878:331; Bates 1882:114.

*Colpodes coeruleus*, Csiki 1931:751; Blackwelder 1944:38.

This distinctive species is widespread in tropical parts of Mexico north of the Isthmus of Tehuantepec.

*Platynus cavatus* (Bates), new combination.

*Anchomenus cavatus* Bates 1882:95. Holotype female, "TYPE H.T.", "Juquila", "Mexico. Salle Coll." (BMNH). Type locality Santa Catarina Juquila, Oaxaca, Mexico.

*Agonum cavatum*, Csiki 1931:846; Blackwelder 1944:41.

This distinctive species is widespread at moderate elevations in Mexico north of the Isthmus of Tehuantepec.

[*Platynus chalcopterus* (Reiche), see *P. purpuratus* (Reiche)].

*Platynus championi* (Bates), new combination.

*Colpodes championi* Bates 1882:107. Lectotype male, here designated, "TYPE H.T.", "Cerro Zunil, 4000' Champion" (BMNH).

*Colpodes championi*, Csiki 1931:750; Blackwelder 1944:38.

*Colpodes euides* Bates 1882:107. Lectotype male, here designated, "TYPE H.T.", "Aceituno, Guatemala Champion" (BMNH). New synonymy.

*Colpodes euides*, Csiki 1931:753; Blackwelder 1944:38.

This otherwise Guatemalan species is known in Mexico only from near Huixtla in extreme southeastern Chiapas. In Guatemala, the name *championi* refers to samples from the southwest, and the name *euides* refers to samples from central and eastern areas; these samples are linked by clear character clines. I found no differences in structures of male genitalia, whereas the form of the apex of the median lobe of the related and sympatric *P. procephalus* is quite different.

*Platynus chaudiroidi* (Coquerel), new combination.

*Colpodes sexpunctatus* Chaudoir 1859:345. Lectotype male, here designated, first of two males and two females labelled "Ex Musaeo Chaudoir" (MNHP 296/6/2). Type locality "Cordova", Veracruz, Mexico.

*Colpodes chaudiroidi* Coquerel 1866:307, new name for *C. sexpunctatus* Chaudoir 1859, preoccupied by *C. sexpunctatus* (Dejean) 1831.

*Colpodes chaudiroidi*, Chaudoir 1878:358; Bates 1882:125; Csiki 1931:750; Blackwelder 1944:38.

This species is closely related to *P. metallicus*. I have seen specimens from various localities in the Mexican state of Veracruz.

[*Platynus chevrolati* (Chaudoir), see *P. acuminatus* (Chevrolat)].

*Platynus (Hemiplatynus) chihuahuae* Bates.

*Platynus chihuahuae* Bates 1884:279. Lectotype male, here designated, "TYPE H.T.", "Pinos Altos, Chihuahua, Mexico. Buchan-Hepburn" (BMNH).

*Hemiplatynus (Hemiplatynus) chihuahuae*, Casey 1920:16.

*Agonum (Hemiplatynus) chihuahuae*, Csiki 1931:849 (*lapsus calami*).

*Agonum chihuahuae*, Blackwelder 1944:41.

This species is known only from the state of Chihuahua. As suggested by Bates, this species, representing subgenus *Hemiplatynus*, is probably closely related to forms placed in subgenus *Rhadine*.

[*Platynus chloreus* (Bates), see *P. monachus* (Dejean)]

*Platynus colibor* Whitehead, new name.

*Colpodes bicolor* Chaudoir 1878:351. Holotype male, "TYPE H.T.", "Type", "Puebla", "Mexico. Salle Coll.", "579" (BMNH).

*Colpodes bicolor*, Bates 1882:124; Csiki 1931:748; Blackwelder 1944:38.

*Platynus bicolor* (Chaudoir) 1878 is preoccupied by *P. bicolor* (LeConte) 1854, a junior synonym of *P. brunneomarginatus* (Mannerheim) of the *P. decentis* group. The specific epithet, *colibor*, here suggested as a replacement name, is an arbitrarily formed anagram of *bicolor*. This species is widespread in low-lands of western Mexico, from Chiapas to Nayarit.

*Platynus columbinus* (Chaudoir), new combination.

*Colpodes columbinus* Chaudoir 1878:332. Lectotype female, here designated, "columbinus in Mexico" (Dejean's script) (MNHP). Type locality "Orizaba", Veracruz, Mexico.

*Colpodes columbinus*, Bates 1882:114; Csiki 1931:751; Blackwelder 1944:38.

This distinctive species is known only from various localities in the vicinity of Cordova, Jalapa, and Orizaba, state of Veracruz.

*Platynus concisus* (Bates), new combination.

*Anchomenus concisus* Bates 1878:594. Lectotype female, here designated, "Mexico City", "Anchom. concisus Bates", "Colpodes angulosus Chd. comp. w. type" (Bates, MNHP).

*Colpodes concisus*, Bates 1882:104; Csiki 1931:751; Blackwelder 1944:38.

*Anchomenus suffectus* Bates 1878:594. Lectotype male, here designated, "Mexico", "Anchom. suffectus Bates" (Bates, MNHP). New synonymy.

*Colpodes suffectus*, Bates 1882:104; Csiki 1931:763; Blackwelder 1944:40.

*Colpodes petilus* Bates 1884:283. Lectotype female, here designated, first specimen labelled "Las Vigas Mexico Hoege", "Colpodes petilus Bates 1891-61", "Colpodes petilus Bates" (BMNH). New synonymy.

This species occurs at higher elevations in central Mexico.

*Platynus conicicollis* (Chaudoir), new combination.

*Colpodes conicicollis* Chaudoir 1878:362. Lectotype male, here designated, first male labelled "Ex Musaeo Chaudoir" (MNHP, 297/1/5). Type locality "Oaxaca", Mexico.

*Colpodes conicicollis*, Bates 1882:128; Csiki 1931:751; Blackwelder 1944:38.

This distinctive species is related to *P. inops*, *P. aeneicauda*, and allies. Specimens have been collected in various localities in the state of Oaxaca.

*Platynus consularis* (Casey), new combination.

*Anchomenus consularis* Casey 1920:33. Lectotype female, here designated, "Mex", "TYPE USNM 47408" (USNM). Type locality "Guerrero", Mexico.

*Agonum consulare*, Csiki 1931:862 (subgenus *Anchomenus*); Blackwelder 1944:41.

This form is evidently quite closely related to *P. porrectus*, and perhaps is conspecific with it. Specimens seen from the state of Hidalgo agree with the holotype of *P. convexulus*.

Specimens from various localities in the Trans-Volcanic Sierra differ by dorsoapical setae on hind femora, and may represent a distinct species.

*Platynus cordatus* (Chaudoir), new combination.

*Colpodes cordatus* Chaudoir 1859:337. Lectotype male, here designated, first male labelled "Ex Musaeo Chaudoir" (MNHP, 296/1/1). Type locality "Toxpam, pres Cordova", Veracruz, Mexico.

*Colpodes cordatus*, Chaudoir 1878:340; Bates 1882:119; Csiki 1931:751; Blackwelder 1944:38.

I have seen specimens definitely referable to this species only from localities near Cordova, Veracruz; records from Guatemala (Bates, 1882) may not pertain to this species. The taxonomic status of this form, a member of the *P. aequinoctialis*–*P. variabilis* complex, is uncertain.

[*Platynus crossomerus* (Chaudoir), new combination].

*Colpodes crossomerus* Chaudoir 1878:331. Holotype female, "Guatemala", "Soc. Ent. Belg. Coll. Putzeys", "C. crossomerus Chaud" (in Chaudoir's script) (IRSB).

*Colpodes crossomerus*, Bates 1882:114; Csiki 1931:751; Blackwelder 1944:38.

This species is not known from Mexico, as only the type specimen is known. It keys to near *P. procephalus* or *P. semiopacus*, and is evidently related to them, with anal setae multiple and dorsoapical setae of hind femur lacking. It differs from *P. procephalus* by narrower lateral pronotal explanation, more broadly rounded elytral apex, and elytron purplish rather than submetallic. It differs from *P. semiopacus* by color, and humeral angle of elytron more obtuse.

*Platynus cupripennis* (Laporte), new combination.

*Dyscolus cupripennis* Laporte 1835:57. Type not found, perhaps in MNHP but not in Oberthür collection. Type locality "Mexique".

*Dyscolus cyanipennis* Chaudoir 1837:12. Lectotype male, here designated, fourth specimen and first male labelled "Ex Musaeo Chaudoir" (MNHP, 295/2/2). Type locality "Mexique". New synonymy.

*Colpodes cyanipennis*, Chaudoir 1859:341; Chaudoir 1878:320; Bates 1882:110; Csiki 1931:752; Blackwelder 1944:38.

*Dyscolus nebrioides* Chaudoir 1837:13. Lectotype male, here designated, fifth specimen and second male labelled "Ex Musaeo Chaudoir" (MNHP, 295/2/1). Type locality "Mexique". New synonymy.

*Colpodes nebrioides*, Chaudoir 1859:342; Chaudoir 1878:320; Bates 1882:110; Csiki 1931:758; Blackwelder 1944:39.

This species is known from various localities in Hidalgo and Veracruz: Orizaba (Chaudoir, 1859), Jacala, and Las Vigas (Bates, 1882). Chaudoir (1859) placed *cupripennis* as a questionable synonym of *nebrioides*; I follow his interpretation, but reverse synonymy according to priority. None of the characters cited by Chaudoir (1837, 1859) to distinguish *nebrioides* from *cyanipennis* are constant, and I therefore suggest the synonymy above. From the literature, I judge the two forms are sympatric; but perhaps typical *cyanipennis* is from around Orizaba, while *nebrioides* occurs further to the north. Further study is needed.

[*Platynus curtipennis* (Casey), see *P. moestus* (Dejean)].

*Platynus cyanides* (Bates), new combination.

*Colpodes cyanides* Bates 1882:112. Holotype male, "TYPE H.T.", "Tocoy Vera Paz Guatemala" (BMNH).

*Colpodes cyanides*, Csiki 1931:752; Blackwelder 1944:38.

I have examined specimens of this distinctive species from localities in the Mexican states of Chiapas, Morelos, and Oaxaca.

[*Platynus cyanipennis* (Chaudoir), see *P. cupripennis* (Laporte)]

*Platynus cycloderus* (Chaudoir), new combination.

*Colpodes cycloderus* Chaudoir 1859:335. Lectotype male(?), here designated, "cycloderus Chaud", "Guatemala Salle" (MNHP, 295/4/5).

*Colpodes tenuicornis*, in part, Chaudoir 1878:321; Bates 1882:114; Csiki 1931:764; Blackwelder 1944:40.

*Colpodes prolongatus* Bates 1882:114. Lectotype female, here designated, "Chontales", "Colpodes prolongatus Bates" (Bates, MNHP). Type locality Chontales, Nicaragua. New synonymy.

*Colpodes prolongatus*, Csiki 1931:760; Blackwelder 1944:40.

*Stenocnemus versicolor* Motschoulsky 1864:308. Type not found, probably in Moscow. New synonymy.

Chaudoir (1878) placed the names *cycloderus* and *versicolor* in synonymy with *tenuicornis*, an arrangement followed by all subsequent workers. However, *P. cycloderus* is distinct from the allopatric *P. tenuicornis*, and specimens of it are distinguished by having only two pairs of marginal pronotal setae. I suggest the synonymy of *C. versicolor* with *P. cycloderus* because a specimen, perhaps a cotype, in the Oberthür collection (MNHP) is labelled "Stenocnemus versicolor Motsch", is placed with specimens of *P. cycloderus*, and is conspecific with them. I cannot distinguish specimens of *C. prolongatus* from those of *P. cycloderus*, hence the synonymy proposed here. I have examined specimens of this species from various localities in Chiapas and southward to Costa Rica.

*Platynus delicatulus* (Chaudoir), new combination.

*Colpodes delicatulus* Chaudoir 1878:323. Lectotype female, here designated, "Mexique", "Ex Musaeo Chaudoir" (MNHP, 295/2/5). Type locality "Mexique".

*Colpodes delicatulus*, Bates 1882:111; Csiki 1931:752; Blackwelder 1944:38. This species is known only from two type specimens.

*Platynus deyrollei* (Chaudoir), new combination.

*Colpodes deyrollei* Chaudoir 1878:336. Holotype female, "Mexique", "A. Deyrolle", "sect. incerta", "Ex Musaeo Chaudoir" (MNHP, 295/5/5). Type locality "Mexique".

*Colpodes deyrollei*, Bates 1882:116; Csiki 1931:752; Blackwelder 1944:38.

This species is known only from the type.

*Platynus dilutus* (Chaudoir), new combination.

*Colpodes dilutus* Chaudoir 1859:332. Lectotype male, here designated, "Ex Musaeo Chaudoir" (MNHP, 296/2/6). Type locality "Toxpan aux environs de Cordova", Veracruz, Mexico.

*Colpodes dilutus*, Bates 1882:120; Csiki 1931:752; Blackwelder 1944:38.

Of four specimens originally reported, I found only one and here designate it as lectotype. I have studied specimens of this species from localities in Oaxaca and Veracruz.

*Platynus (Platynella) districtus* (Casey), new combination.

See Barr (1970) for synonymic list and further information. The name *Bolivaridius ova-tellus* Straneo is a synonym.

*Platynus dominicensis* (Bates), new combination.

*Anchomenus dominicensis* Bates 1882:96. Lectotype male, here designated, selected by R. B. Madge, "LECTOTYPE" (disc), "Cordova", "Mexico. Salle Coll.", "510", "B. C. A. Col. I. 1. *Anchomenus dominicensis*, Bates", "Platynus dominicensis, Mann. apud. Salle.", "LECTOTYPE *Anchomenus dominicensis* Bates designated R. B. Madge '72" (BMNH).

*Agonum dominicense*, Csiki 1931:847; Blackwelder 1944:41.

I have examined specimens of this species from various localities in the Mexican states of Oaxaca and Veracruz, and from various localities in Central America south to Panama. This species is a member of a poorly understood complex, most of whose components are undescribed.

*Platynus durangensis* (Bates), new combination.

*Colpodes durangensis* Bates 1882:105. Lectotype male, here designated, selected by G. E. Ball, "Ciudad, Durango, Höge", "Colpodes durangensis Bates", "LECTOTYPE" (disc) "Ball desig. '72" (BMNH).

*Colpodes durangensis*, Csiki 1931:752; Blackwelder 1944:38.

I have examined specimens of this species from several localities at high elevations in Durango. *Platynus valens* is related and quite similar, but is sympatric and evidently distinct.

*Platynus ebeninus* (Chaudoir), new combination.

*Colpodes ebeninus* Chaudoir 1878:310. Holotype female, "TYPE H.T.", "Type", "Santecomapan", "Mexico. Salle Coll." (BMNH). Type locality Santecomapan, Veracruz, Mexico.

*Colpodes ebeninus*, Bates 1882:109; Csiki 1931:752; Blackwelder 1944:38.

This species is so far known only from the type specimen, from lowland rain forest in the state of Veracruz. Guerrero specimens under this name in Bates (MNHP) and Biologia (BMNH) collections belong to *P. consularis*, a species similar in some characteristics but only distantly related to *P. ebeninus*.

*Platynus erythrocerus* (Chaudoir), new combination.

*Colpodes erythrocerus* Chaudoir 1859:348. Lectotype female, here designated, first female labelled "Ex Musaeo Chaudoir" (MNHP, 296/6/6).

*Colpodes erythrocerus*, Chaudoir 1878:359; Bates 1882:126; Csiki 1931:753; Blackwelder 1944:38.

No type locality was specified for this distinctive species. I have examined specimens from the states of Oaxaca and Veracruz.

[*Platynus euides* (Bates), see *P. championi* (Bates)]

*Platynus (Rhadine) euprepes* Bates.

*Platynus euprepes* Bates 1882:93. Lectotype female, here designated, "TYPE H.T.", "Ciudad, Mex., 8100 ft. Forrer", "82" (BMNH).

*Agonum euprepes*, Csiki 1931:849 (subgenus *Rhadine*); Blackwelder 1944:41.

I have examined specimens of this species from several localities at high elevations in the state of Durango. Of some five epigeal Mexican *Rhadine* species seen by me, this is the most distinctive.

[*Platynus evanescens* (Bates), new combination].

*Colpodes evanescens* Bates 1882:108. Lectotype female, here designated, left female of two pinned together, "TYPE H.T.", "Totonacapan, 85-10,500 ft. Champion" (BMNH).

*Colpodes evanescens*, Csiki 1931:753; Blackwelder 1944:38.

This species, described from Guatemala, is not known from Mexico.

*Platynus falli* (Darlington), new combination.

*Colpodes falli* Darlington 1936:152. Holotype male from "Baboquivari Mts., Arizona" (MCZ).

*Colpodes falli*, Blackwelder 1939:14

This species will no doubt be found to occur in northwestern Mexico. It is closely related to *P. segregatus* and perhaps the two are conspecific.

*Platynus femoralis* (Chaudoir), new combination.

*Colpodes femoralis* Chaudoir 1878:341. Lectotype female, here designated, "Ex Musaeo Chaudoir" (MNHP, 296/2/3). Type locality "Oaxaca", Mexico.

*Colpodes femoralis*, Bates 1882:119; Csiki 1931:753; Blackwelder 1944:38.

I have examined specimens of this distinctive species from various localities in central Mexico. Further study is required to determine whether forms without posterior pronotal setae (Jalisco, Mexico, Oaxaca) are reproductively isolated from forms with posterior pronotal setae (Morelos).

*Platynus forreri* (Bates), new combination.

*Colpodes forreri* Bates 1882:109. Lectotype male, here designated, "TYPE H.T.", "Ciudad, Mex., 8100 ft Forrer" (BMNH). Type locality Ciudad, Durango, Mexico.

*Colpodes forreri*, Csiki 1931:753; Blackwelder 1944:38.

I have examined specimens of this species from various high altitude locations in the state of Durango.

[*Platynus fragilis* (Chaudoir), see *P. lifragis* Whitehead].

*Platynus fratellus* (Chaudoir), new combination.

*Colpodes fratellus* Chaudoir 1878:358. Holotype male, "Cordova", "Mexico. Salle Coll." (BMNH). Type locality originally given as "Mexique", here restricted to Cordova, Veracruz, Mexico; this is in contradiction to Bates' (1882) indication of Oaxaca as type locality, but I found no other specimen that might represent Chaudoir's original example.

*Colpodes fratellus*, Bates 1882:126; Csiki 1931:753; Blackwelder 1944:39.

*Colpodes jalapensis* Bates 1882:126. Lectotype male, here designated, selected by G. E. Ball, "Jalapa Mexico Hoege" and "Ball desig." (BMNH). New synonymy.

*Colpodes jalapensis*, Csiki 1931:755; Blackwelder 1944:39.

*Colpodes trujilloi* Bates 1891:259. Lectotype female, here designated, "TYPE H.T.", "Jalapa, Mexico M. Trujillo" (BMNH). New synonymy.

*Colpodes trujilloi*, Csiki 1931:764; Blackwelder 1944:40.

I have examined specimens of this species from the states of Campeche, Chiapas, Oaxaca,



Tamaulipas, and Veracruz. This material is varied, and encompasses all three named forms; I therefore propose the synonymies above. Specimens referable to *fratellus* tend to have elytral microsculpture dense, color more metallic, pronotal front angle less prominent, lateral pronotal explanation broader, and frons with reduced microsculpture. Specimens of *trujilloi* are smaller, darker, and shinier. Specimens of *jalapensis* are the size of *fratellus*, but less metallic, duller, and otherwise contrasted as above. I am unable to find any constant differences. The group is, however, in need of study.

[*Platynus funestus* (Chaudoir), see *P. moestus* (Dejean)]

*Platynus gracilis* (Chaudoir), new combination.

*Colpodes gracilis* Chaudoir 1859:330. Lectotype female, here designated, "Ex Musaeo Chaudoir" (MNHP, 296/2/4). Type locality "Mexique".

*Colpodes gracilis*, Chaudoir 1878:342; Bates 1882:120; Csiki 1931:754; Blackwelder 1944:39.

It is not clear from the original description whether Chaudoir had one specimen or more than one. I suspect that this species occurs in the state of Veracruz.

[*Platynus guatemalensis* (Chaudoir), new combination].

*Colpodes guatemalensis* Chaudoir 1878:298. Holotype female, "Guatemala", "Soc. Ent. Belg. Coll. Putzeys" (IRSB).

*Colpodes guatemalensis*, Bates 1882:103; Csiki 1931:754; Blackwelder 1944:39.

This Guatemalan species is not known from Mexico, and is not closely related to any known Mexican species.

[*Platynus guerrerensis* (Casey), see *P. variabilis* (Chaudoir)]

*Platynus haptoderoides* (Bates), new combination.

*Colpodes haptoderoides* Bates 1891:252. Lectotype female, here designated, "Omilteme . . .", "Sp. figured" (BMNH).

*Colpodes haptoderoides*, Csiki 1931:754; Blackwelder 1944:39.

This species is presently known from just two localities in the state of Guerrero.

[*Platynus harfordi* (Casey), see *P. obscurellus* (Bates)]

*Platynus harpaloides* (Bates), new combination.

*Colpodes harpaloides* Bates 1891:253. Lectotype male, here designated, "TYPE H.T.", "Omilteme ..." (BMNH).

*Colpodes harpaloides*, Csiki 1931:754; Blackwelder 1944:39.

This species is known only from the type locality, in Guerrero.

[*Platynus hondurae* (Bates), see *P. procephalus* (Bates)]

*Platynus ilagis* Whitehead, new name.

*Colpodes agilis* Chaudoir 1878:330. Lectotype male, here designated, "Huachinango", "11<sup>e</sup> sect. A.b.", "Ex Musaeo Chaudoir" (MNHP, 295/4/3).

*Colpodes agilis*, Bates 1882:113; Csiki 1931:747; Blackwelder 1944:37.

The taxonomic status and relationships of this species are uncertain; it appears closely related to *P. laetiusculus*. As the epithet *agilis* Chaudoir 1878 is preoccupied in *Platynus* by

*agilis* LeConte 1863, I here propose the replacement name *ilagis*, an arbitrarily formed anagram.

[*Platynus incommodus* (Chaudoir), see *P. obscurellus* (Bates)].

[*Platynus infidus* (Casey), see *P. nitidus* (Chaudoir)].

*Platynus inops* (Chaudoir), new combination.

*Colpodes inops* Chaudoir 1878:363. Lectotype male, here designated, first male labelled "Ex Musaeo Chaudoir" (MNHP, 297/1/6). Type locality "Oaxaca".

*Colpodes inops*, Bates 1882:128; Csiki 1931:755; Blackwelder 1944:39.

This form and the related *P. aeneicauda* are allopatric, and may be conspecific. Known Mexican localities are in the states of Chiapas and Oaxaca.

*Platynus iricolor* (Bates), new combination.

*Colpodes iricolor* Bates 1882:129. Lectotype male, here designated, "TYPE H.T.", "Cerro Zunil 4-5000 ft. Champion" (Guatemala) (BMNH).

*Colpodes iricolor*, Csiki 1931:755; Blackwelder 1944:39.

This species is related to *P. quadrilaterus* and is allopatric to it, but is evidently not conspecific. In Mexico, this species is known only from the state of Chiapas.

[*Platynus jalapensis* (Bates), see *P. fratellus* (Chaudoir)].

*Platynus laetiusculus* (Chaudoir), new combination.

*Colpodes laetiusculus* Chaudoir 1878:329. Holotype male, "Juquila", "Mexico. Salle Coll.", "549", "C. laetiusculus Chaud" (BMNH).

*Colpodes laetiusculus*, Bates 1882:113; Csiki 1931:755; Blackwelder 1944:39.

This species is known only from the type, from a locality in the Sierra Madre del Sur of Oaxaca.

*Platynus (Rhadine) leptodes* Bates.

*Platynus leptodes* Bates 1882:92. Lectotype male, here designated, selected by G.E. Ball, "TYPE H.T.", "Ciudad, Mex., 8100 ft. Forrer", "276" (BMNH).

*Agonum leptodes*, Csiki 1931:849 (Subgenus *Rhadine*); Blackwelder 1944:42.

This is one of several small epigeal forms of *Rhadine* endemic to northwestern Mexico; it is known only from high altitudes in the state of Durango.

*Platynus lifragis* Whitehead, new name.

*Colpodes fragilis* Chaudoir 1878:329. Holotype female, "Ex Musaeo Chaudoir" (MNHP, 295/4/2). Type locality "Mexico".

*Colpodes fragilis*, Bates 1882:113; Csiki 1931:753; Blackwelder 1944:38.

In Mexico, this species is known only from the state of Chiapas. As the epithet *fragilis* Chaudoir 1878 is preoccupied in *Platynus* by *fragilis* LeConte 1854, I here propose replacement by the arbitrarily formed anagram *lifragis*.

*Platynus limbicollis* (Chaudoir), new combination.

*Colpodes limbicollis* Chaudoir 1878:363. Lectotype female, here designated, first female labelled "Ex Musaeo Chaudoir" (MNHP, 297/1/7). Type locality "Oaxaca", Mexico.

*Colpodes limbicollis*, Bates 1882:128; Csiki 1931:756; Blackwelder 1944:39.

This species is known definitely only from the type specimens, as I did not confirm other records (Bates, 1882).

*Platynus logicus* (Casey), new combination.

*Anchomenus (Platynella) logicus* Casey 1920:24. Holotype female, "Tres Marias, Mor.", "USNM TYPE 47394" (USNM).

*Agonum logicum*, Csiki 1931:849 (subgenus *Platynella*); Blackwelder 1944:42.

This species is known from the states of Mexico and Morelos. It is closely related to but sympatric with *P. nitidus*.

[*Platynus longiceps* Schaeffer, see *P. megalops* (Bates)]

*Platynus longipes* (Chaudoir), new combination.

*Colpodes longipes* Chaudoir 1878:333. Holotype male, "TYPE H.T", "Cuernavaca", "Mexico. Salle Coll." (BMNH). Type locality cited as "pris a Puebla", in contradiction to type label; otherwise, however, indications are that this specimen is the type.

*Colpodes longipes*, Bates 1882:115; Csiki 1931:756; Blackwelder 1944:39.

I have examined specimens of this distinctive species from various localities in the states of Colima, Guerrero, Jalisco, Morelos, and Nayarit.

*Platynus lucilius* (Bates), new combination.

*Colpodes lucilius* Bates 1884:284. Holotype female, "TYPE H.T". "Cordova", "Mexico. Salle Coll." (BMNH).

*Colpodes lucilius*, Csiki 1931:756; Blackwelder 1944:39.

This distinctive species is known only from localities in the states of Oaxaca and Veracruz.

*Platynus lugens* (Dejean), new combination.

*Feronia lugens* Dejean 1831:771. Holotype male, "Feronia", "lugens m in "Mexico", "D. Höpfner", "Ex Musaeo Chaudoir" (first three labels in Dejean script) (MMHP, 294/1/3). Type locality "Mexico".

*Colpodes lugens*, Chaudoir 1878:297; Bates 1882:103; Csiki 1931:756; Blackwelder 1944:39.

*Dyscolus anchomenoides* Chaudoir 1835:440. Holotype female, "anchomenoides (Dyscolus) Chd.", "Ex Musaeo Chaudoir" (MNHP, 294/1/3). Type locality "Mexique".

*Colpodes anchomenoides*, Chaudoir 1859:310.

*Colpodes brunnipennis* Chaudoir 1859:312. Lectotype male, here designated, "brunnipennis Chaud", "Salle", "Ex Musaeo Chaudoir" (MNHP, 294/1/3). Type locality "Orizaba" (?), Veracruz, Mexico.

This species is abundant in the states of Mexico and Morelos, where it is sympatric with *P. moestus*. I have not seen specimens from Veracruz; the record for Orizaba may apply to *P. moestus*, and most probably not all of Chaudoir's original specimens of *brunnipennis* were from there. The specimen selected as lectotype of *P. brunnipennis* clearly is conspecific with *P. lugens*, and is the only specimen in the Oberthür collection labelled as *brunnipennis*.

[*Platynus lymphaticus* (Casey), see *P. nugax* (Bates)]

*Platynus lyratus* (Chaudoir), new combination.

*Colpodes lyratus* Chaudoir 1878:347. Lectotype male, here designated, first male labelled "Ex Musaeo Chaudoir" (MNHP, 296/3/5); box label reads "lyratus Chaudoir, Mexique, Capulalpam, Salle".

*Colpodes lyratus*, Bates 1882:121; Csiki 1931:757; Blackwelder 1944:39.

*Anchomenus pinalicus* Casey 1920:42. Holotype male, "Pinal Mts Arizona, Wickham", "CASEY bequest 1925", "TYPE USNM 47415", "pinalicus Csy." (USNM). New synonymy.

*Anchomenus pinalicus*, Leng and Mutchler 1927:11.

*Agonum pinalicum*, Csiki 1931:861 (subgenus *Anchomenus*).

This widespread species belongs to a complex which requires study. I have seen specimens from the states of Arizona and Queretaro in the north, south to the state of Oaxaca.

*Platynus lyrophorus* (Chaudoir), new combination.

*Colpodes lyrophorus* Chaudoir 1878:319. Lectotype male, here designated, "6<sup>e</sup> sect.", "Ex Musaeo Chaudoir" (MNHP, 295/1/6). Type locality "Mexique".

*Colpodes lyrophorus*, Bates 1882:110; Csiki 1931:757; Blackwelder 1944:39.

This species is known only from the state of Veracruz.

*Platynus macrours* (Chaudoir), new combination.

*Colpodes macrours* Chaudoir 1878:328. Lectotype male, here designated, "Chiapas 5-7-58", "Soc. Ent. Belg. Coll. Putzeys", "C. macrours Chaud" (in Chaudoir script) (IRSB). *Colpodes macrours*, Bates 1882:113; Csiki 1931:757; Blackwelder 1944:39.

This species is known from various localities in the central highlands of the state of Chiapas.

*Platynus marginicollis* (Chaudoir), new combination.

*Colpodes marginicollis* Chaudoir 1859:312. Holotype female, "Ex Musaeo Chaudoir" (MNHP, 294/1/2). Type locality "ecorces a Cordova".

*Colpodes marginicollis*, Chaudoir 1878:295; Bates 1882:102; Csiki 1931:757; Blackwelder 1944:39.

This species has been reported from Cordova, Veracruz (Chaudoir, 1859) and Jacala, Hidalgo (Bates, 1882).

*Platynus (Rhadine) medillini* (Bolivar and Hendrichs), new combination.

See Bolivar and Hendrichs, 1964.

*Platynus megalops* (Bates), new combination.

*Colpodes megalops* Bates 1882:116. Lectotype male, here designated, "TYPE H.T.", "Guanajuato", "Mexico. Salle Coll." (BMNH).

*Colpodes megalops*, Csiki 1931:757; Blackwelder 1944:39.

*Platynus (Colpodes) longiceps* Schaeffer 1910:394. Lectotype female, here designated, "Type", "Huach Mts. Ariz.", "BROOKLYN MUSEUM COLL 1929", "Catal. No. 3195", "Cotype No. 42502 U.S.N.M.", "P. longiceps Schaffer", "Colpodes longiceps (Schfr.) prov. lectot. det. Val. 42" (USNM). New synonymy.

*Platynus (Colpodes) longiceps*, Leng 1920:64.

*Anchomenus (Plocodes) longiceps*, Casey 1920:29

*Colpodes longiceps*, Csiki 1931:756.

I have seen specimens of this species from various western localities from Arizona to Oaxaca. Legs vary from blue to red, are red in the types of *P. megalops* and *P. longiceps*. A male in MNHP, also with red legs, is labelled "parallelipennis Chaud Guanajuato", "inedit.", "Ex Musaeo Chaudoir".

*Platynus melanocnemis* (Chaudoir), new combination.

*Colpodes melanocnemis* Chaudoir 1878:335. Lectotype female, here designated, "Costa Rica", "Soc. Ent. Belg. Coll. Putzeys", "melanocnemis Chaud" (Chaudoir script) (IRSB).

*Colpodes melanocnemis*, Bates 1882:116; Csiki 1931:757; Blackwelder 1944:39.

I have examined Mexican specimens from the states of Chiapas, Guerrero, and Oaxaca. I judge that these specimens are conspecific with those seen from Guatemala and Costa Rica, but the species is at least strongly varied geographically. All Mexican specimens were taken at relatively high elevations.

[*Platynus meridanus* (Chaudoir), new combination].

According to J. Nègre (*in litt.*), this species was described from Merida, Venezuela, not Merida, Yucatan. It is not known from Mexico.

*Platynus metallicus* (Chaudoir), new combination.

*Colpodes metallicus* Chaudoir 1859:345. Lectotype male, here designated, third specimen labelled "Ex Musaeo Chaudoir" (MNHP, 296/6/3); a female labelled "Mex", "metallicus Chaud An. Soc. Ent. 1859 345", "Ex Musaeo Salle 1897" (MNHP, 296/6/3) probably was not examined by Chaudoir. Type locality "Cordova", Veracruz, Mexico.

*Colpodes metallicus*, Chaudoir 1878:358; Bates 1882:125; Csiki 1931:757; Blackwelder 1944:39.

This species has been collected at various localities in the state of Veracruz.

*Platynus minimus* (Bates), new combination.

*Colpodes minimus* Bates 1884:283. Lectotype male, here designated, "TYPE H.T.", "Sp. figured", "Jacala", "Mexico. Salle Coll." (BMNH).

*Colpodes minimus*, Csiki 1931:757; Blackwelder 1944:39.

This species is known only from the type locality.

*Platynus moestus* (Dejean), new combination.

*Feronia moesta* Dejean 1831:770. Holotype female, "♀" *Feronia*", "moesta m in Mexico", "Höpfner", "Ex Musaeo Chaudoir" (MNHP, 294/1/4).

*Colpodes moestus*, Chaudoir 1859:313; Chaudoir 1878:297; Bates 1882:103; Csiki 1931:757; Blackwelder 1944:39.

*Feronia funesta* Chaudoir 1837:31. Lectotype male, here designated, "funestus Chaud", "Ex Musaeo Chaudoir" (MNHP, 294/1/4). Type locality "Mexique".

*Feronia opaca* Chaudoir 1837:32. Lectotype male, here designated, "opacus Chd Chevrolat", "Ex Musaeo Chaudoir" (MNHP, 294/4/4). Type locality "Mexique".

*Colpodes tristis* Chaudoir 1859:314. Holotype male, "var tristis Chaud", "Mexique", "Ex Musaeo Chaudoir" (MNHP, 294/1/4). Type locality "Mexique".

*Anchomenus (Plantys) curtippennis* Casey 1920:27. Lectotype male, here designated, "Tres Marias, Mor.", "TYPE USNM 47392". New synonymy.

*Agonum curtipenne*, Csiki 1931:850 (subgenus *Plantys*); Blackwelder 1944:41.

This species is widespread across the Trans-Volcanic Sierra of central Mexico; in parts of its range it is sympatric with the related *P. lugens*. A female in the Chaudoir collection (MNHP) labelled "montana Chevrolat" is conspecific.

*Platynus monachus* (Dejean), new combination.

*Feronia monacha* Dejean 1831:772. Lectotype female, here designated, selected by G. E. Ball, "Monacha m. in Mexico, Höpfner" (Dejean script), "LECTOTYPE ♀ *Feronia monacha* Dejean, det. G. E. Ball '72" (MNHP, 289/5/6).

*Colpodes monachus*, Bates 1882:115; Csiki 1931:758; Blackwelder 1944:39.

*Colpodes chloreus*, Bates 1882:115. Lectotype male, here designated, "TYPE H.T.", "Cuernavaca", "Mexico. Salle Coll." (BMNH). New synonymy.

*Colpodes choreus*, Csiki 1931:750; Blackwelder 1944:38.

I have examined specimens of this species from numerous localities along the Trans-Volcanic Sierra of central Mexico. The type specimen of *P. monachus* is of the more brightly colored, wing-dimorphic eastern form from Morelos and Puebla, and this is unquestionably conspecific with *P. chloreus*. In more western localities, specimens are darker, brachypterous, and have higher frequency of dorsoapical setae on hind femora; these correspond to Bates' (1882) interpretation of *monachus*. Further study is required to determine whether eastern and western forms are conspecific.

*Platynus (Platynella) montezumae* (Bates), new combination.

See Barr (1970) for synonymic list and other details; no other names are currently considered synonymous. Lectotype male, here designated, selected by G. E. Ball, "Mexico (City)", "Anchom. montezumae Bates", "LECTOTYPE" (disc), "Ball det 72" (Bates, MNHP).

[*Platynus morelosensis* (Casey), see *P. nitidus* (Chaudoir)].

[*Platynus nebrioides* (Chaudoir), see *P. cupripennis* (Laporte)].

[*Platynus neglectus* (Chaudoir), see *P. nugax* (Bates)].

*Platynus niger* (Chaudoir), new combination.

*Colpodes niger* Chaudoir 1859:352. Lectotype male, here designated, first specimen labelled "Ex Musaeo Chaudoir" (MNHP, 295/6/2). Type locality "pres d'Orizaba", Veracruz, Mexico.

*Colpodes niger*, Chaudoir 1878:337; Bates 1882:117; Csiki 1931:758; Blackwelder 1944:39.

I have examined specimens of this species from various localities in Veracruz. The Colombian species *P. punctatostriatus* (Chaudoir 1878:337), new combination, is closely related, but lacks frontal microsculpture and has elytral striae evidently punctate at least to posterior puncture of interval three; lectotype female, here designated, "12<sup>e</sup> s.A.b.2", "Ex Musaeo Chaudoir", "punctatostriatus type Chaud." (MNHP).

*Platynus nitidus* (Chaudoir), new combination.

*Dyscolus nitidus* Chaudoir 1837:8. Lectotype male, here designated, selected by G. E. Ball, "Ex Musaeo Chaudoir", "LECTOTYPE" (disc), "Dyscolus nitidus Chaud. det. G. E. Ball '72" (MNHP). Type locality Mexico, not further specified.

*Colpodes nitidus*, Chaudoir 1849:319; Chaudoir 1878:346; Bates 1882:120; Csiki 1931:758; Blackwelder 1944:39.

*Colpodes planicollis* Chaudoir 1859:320. Holotype female, "planicollis Chaud", "Mexique Dohrn", "Ex Musaeo Chaudoir" (MNHP). Synonymy by Chaudoir (1878).

*Colpodes stenos* Bates 1891:256. Lectotype female, here designated, "TYPE H.T.", "Toluca, Mexico Höge" (BMNH). New synonymy.

*Colpodes stenos*, Csiki 1931:763; Blackwelder 1944:40.

*Anchomenus (Platynella) morelosensis* Casey 1920:25. Holotype female, "Tres Marias, Mor.", "USNM TYPE 47396" (USNM). New synonymy.

*Agonum morelosense*, Csiki 1931:849 (subgenus *Platynella*). Blackwelder 1944:42.

*Anchomenus (Platynella) infidus* Casey 1920:26. Holotype female, "Tres Marias, Mor.", "USNM TYPE 47397" (USNM). New synonymy.

*Agonum infidum*, Csiki 1931:849 (subgenus *Platynella*); Blackwelder 1944:42.

This species, widespread in the Transvolcanic Sierra of central Mexico, is strongly marked by geographic variation and therefore deserves detailed study. One male in the Chaudoir collection (MNHP) is labelled "*Anchomenus*", "*chevrolatii* mihi *Dyscolus angusticollis* Chevrol. h. Mexico D. Chevrolat", and "Ex Musaeo Chaudoir". These non-validated names were treated as synonyms of *C. nitidus* by Chaudoir (1878), and the specimen is the one Dejean (1831) referred to as "*chevrolatii*".

*Platynus nugax* (Bates), new combination.

*Anchomenus nugax* Bates 1878:594. Lectotype male, here designated, "Mexico City", "Anchom. nugax Bates", "neglectus Chd. comp. type" (Bates, MNHP).

*Colpodes nugax*, Bates 1882:104; Csiki 1931:758; Blackwelder 1944:39.

*Colpodes neglectus* Chaudoir 1878:298. Holotype male, "Ex Musaeo Chaudoir" (MNHP, 294/2/1). Synonymy by Bates (1882).

*Anchomenus simplicior* Bates 1878:595. Lectotype male, here designated, first male labelled "Mexico City", "Anchom. simplicior Bates" (Bates, MNHP). New synonymy.

*Colpodes simplicior*, Bates 1882:104; Csiki 1931:763; Blackwelder 1944:40.

*Anchomenus lymphaticus* Casey 1920:44. Holotype male, "Mex DF", USNM TYPE 47418" (USNM). New synonymy.

*Agonum lymphaticum*, Csiki 1931:863; Blackwelder 1944:42.

This species is widespread in the Transvolcanic Sierra of central Mexico, is geographically varied, and is worthy of detailed study. Differences exhibited by the type specimens of *nugax*, *neglectus*, *simplicior*, and *lymphaticus* are attributed to this geographic variation.

*Platynus nyctimus* (Bates), new combination.

*Colpodes nyctimus* Bates 1884:282. Lectotype female, here designated, "Tenancingo Mexico", "Colpodes nyctimus Bates" (Bates, MNHP).

*Colpodes nyctimus*, Csiki 1931:758; Blackwelder 1944:39.

I have examined specimens of this species from the states of Guerrero and Mexico.

*Platynus obscurellus* (Bates), new combination.

*Colpodes obscurellus* Bates 1878:596. Lectotype male, here designated, "Irazu 6-7000 ft. H. Rogers", "Colpodes atratus Chd.", "Colpodes obscurellus Bates" (BMNH). Type locality Irazu, Costa Rica. Bates (1882) placed this name as a junior synonym of *C. atratus* Chaudoir 1859, but I here reverse the synonymy as the latter is a junior homonym of *atratus* Blanchard 1853.

*Colpodes atratus* Chaudoir 1859:323. Lectotype (sex?), here designated, selected by G. E. Ball, "Ex Musaeo Chaudoir" (MNHP, 296/3/7); this specimen is broken, only the mentum remaining in association with the pin. Type locality "Colombie". Two Colombian species are confused under the name *C. atratus* in the Oberthür collection; specimens of one are evidently conspecific with Mexican specimens, and I therefore follow Bates' (1882) interpretation except that I reverse synonymy for reasons given above. New synonymy.

*Colpodes atratus*, Bates 1882:122; Csiki 1931:748; Blackwelder 1944:38.

*Colpodes incommodus* Chaudoir 1878:347. Lectotype female, here designated, "Chiapas", "Mexico. Salle Coll.", "*Colpodes incommodus* Chd" (BMNH); this selection is based on male and female specimens in BMNH, both from Sallé material; I judge that Chaudoir erred in ascribing these specimens to Putzeys, as I found no type specimens of *C. incommodus* in IRSB material. Type locality "Chiapas", Mexico. New synonymy.

*Colpodes incommodus*, Bates 1882:121; Csiki 1931:755; Blackwelder 1944:39.

*Anchomenus harfordi* Casey 1920:42. Lectotype male, here designated, "Guer.", "USNM TYPE 47417" (USNM). New synonymy.

*Agonum harfordi*, Csiki 1931:863 (subgenus *Anchomenus*); Blackwelder 1944:42.

Known Mexican localities for this species are in the states of Chiapas and Guerrero. My judgements about synonymies proposed here are tentative, as this species is quite varied geographically.

*Platynus obscurus* (Chaudoir), new combination.

*Colpodes obscurus* Chaudoir 1859:322. Lectotype male, here designated, first specimen labelled "Ex Musaeo Chaudoir" (MNHP, 296/3/6). Type locality Orizaba, Veracruz, Mexico.

*Colpodes obscurus*, Chaudoir 1878:347; Bates 1882:121; Csiki 1931:759; Blackwelder 1944:39.

This species is known from various localities in the states of Chiapas and Veracruz.

*Platynus olivaceus* (Chaudoir), new combination.

*Colpodes olivaceus* Chaudoir 1878:328. Lectotype female, here designated, "Mexique", "A. Deyrolle", "Ex Musaeo Chaudoir" (MNHP, 295/3/6). Type locality "Oaxaca", Mexico.

*Colpodes olivaceus*, Bates 1882:113; Csiki 1931:759; Blackwelder 1944:39.

This species is known from various localities in the states of Chiapas and Veracruz.

*Platynus omaseoides* (Bates), new combination.

*Colpodes omaseoides* Bates 1891:255. Lectotype male, here designated, "Omiteme Guerrero 8000 ft. Aug. H. H. Smith", "Sp. figured", "Tr. Ent. S. L. 1891 *Colpodes omaseoides* Bates" (BMNH).

*Colpodes omaseoides*, Csiki 1931:759; Blackwelder 1944:39.

This species is known only from the type locality.

[*Platynus opacus* (Chaudoir), see *P. moestus* (Dejean)].

*Platynus orbicollis* (Chaudoir), new combination.



*Colpodes orbicollis* Chaudoir 1859:346. Lectotype female, here designated, "Sta Comapan Salle", "Ex Musaeo Chaudoir" (MNHP, 296/6/4). Type locality Sontecomapan, Veracruz, Mexico.

*Colpodes orbicollis*, Chaudoir 1878:358; Bates 1882:125; Csiki 1931:759; Blackwelder 1944:39.

I have examined specimens of this species from various localities in southern Mexico, states of Chiapas, Oaxaca, and Veracruz.

[*Platynus ovatellus* (Straneo), see *P. districtus* (Casey)].

*Platynus ovatulus* (Bates), new combination.

*Anchomenus ovatulus* Bates 1884:281. Lectotype female, here designated, "TYPE H.T.", "Pinos Altos, Chihuahua, Mexico Buchan-Hepburn" (BMNH).

*Agonum ovatulum*, Csiki 1931:847; Blackwelder 1944:42.

Known from various localities in Arizona and Chihuahua, this species belongs to a large complex most components of which remain undescribed.

*Platynus pallidipes* (Chaudoir), new combination.

*Dyscolus (Stenocnemus) pallidipes* Chaudoir 1850:381. Lectotype female, here designated, fungus-covered specimen, "Ex Musaeo Chaudoir" (MNHP, 295/5/3). Type locality "Mexique".

*Colpodes pallidipes*, Chaudoir 1859:339; Chaudoir 1878:335; Bates 1882:116; Csiki 1931:759; Blackwelder 1944:39.

I have examined numerous specimens of this highly distinctive species from various localities in the states of Chiapas and Veracruz. An apparently related, undescribed species from Costa Rica differs by elytra metallic blue.

[*Platynus parviceps* (Bates), new combination].

*Colpodes parviceps* Bates 1878:597. Lectotype male, here designated, selected by G. E. Ball, "Chontales", "Colpodes parviceps Bates", "desig. G. E. Ball '72" (Bates, MNHP). Type locality Chontales, Nicaragua.

This species is not known from Mexico. Specimens reported by Bates (1882) from British Honduras and Guatemala do not pertain to *P. parviceps*, but do agree with specimens of an undescribed form from southern Mexico.

*Platynus pectoralis* (Chaudoir), new combination.

*Colpodes pectoralis* Chaudoir 1878:353. Holotype female, "Ex Musaeo Chaudoir" (MNHP, 296/5/4). Type locality "Orizaba", Veracruz, Mexico.

*Colpodes pectoralis*, Bates 1882:124; Csiki 1931:759; Blackwelder 1944:39.

This species is known from the type specimen only.

*Platynus (Rhadine) perlevis* (Casey), new combination.

*Rhadine perlevis* Casey 1913:168. Holotype female, "Mex", "CASEY bequest 1925", "perlevis Csy.", "TYPE USNM 35023". Type locality Colonia Garcia, Sierra Madre Mts, Chihuahua, Mexico.

*Agonum perleve*, Csiki 1931:849 (subgenus *Rhadine*); Blackwelder 1944:42.

This species is one of a complex of small epigeal *Rhadine* from northwestern Mexico.

[*Platynus petilus* (Bates), see *P. concisus* (Bates)].

*Platynus phaeolomus* (Chaudoir), new combination.

*Colpodes phaeolomus* Chaudoir 1878:357. Holotype female, "TYPE H.T.", "Type", "Santecomapan", "Mexico. Salle Coll.", "581", "C. phaeolomus Chaud" (BMNH). Type locality Sontecomapan, Veracruz, Mexico.

*Colpodes phaeolomus*, Bates 1882:125; Csiki 1931:760; Blackwelder 1944:39.

Known Mexican localities for this species are in the states of Campeche, Chiapas, San Luis Potosi, Tamaulipas, and Veracruz.

*Platynus picicornis* (Chaudoir), new combination.

*Colpodes picicornis* Chaudoir 1878:350. Lectotype male, here designated, "12<sup>e</sup> Sect. A. b. 2". "Anchomenus", "picicornis m. Mexico", "Ex Musaeo Chaudoir" (MNHP, 296/4/5). Type locality "Mexique".

*Colpodes picicornis*, Bates 1882:123; Csiki 1931:760; Blackwelder 1944:40.

I have examined specimens of this species from various localities in Oaxaca and Veracruz.

[*Platynus pinalicus* (Casey), see *P. lyratus* (Chaudoir)].

[*Platynus planicollis* (Chaudoir), see *P. nitidus* (Chaudoir)].

*Platynus platysmoides* (Bates), new combination.

*Colpodes platysmoides* Bates 1891:254. Lectotype male, here designated, "Xautipa Guerrero H. H. Smith", "Sp. figured" (BMNH).

*Colpodes platysmoides*, Csiki 1931:760; Blackwelder 1944:40.

This distinctive species is probably closely related to *P. harpaloides*; I have examined specimens from Omilteme (1, BMNH), Xautipa (2, BMNH; 1, MNHP), and Chilpancingo (1, MNHP), all in the state of Guerrero.

*Platynus porrectus* (Chaudoir), new combination.

*Colpodes porrectus* Chaudoir 1878:326. Lectotype male, here designated, "Mexique", "A. Deyrolle", "Ex Musaeo Chaudoir" (MNHP, 295/3/5). Type locality "Mexique".

*Colpodes porrectus*, Bates 1882:112; Csiki 1931:760; Blackwelder 1944:40.

The taxonomic relationships of this species are unclear; *P. convexulus* may be a synonym.

*Platynus pristonychoides* (Chaudoir), new combination.

*Colpodes pristonychoides* Chaudoir 1878:321. Holotype male, "TYPE H.T.", "Type", "Yolotepec", "Mexico. Salle Coll.", "536" (BMNH).

*Colpodes pristonychoides*, Bates 1882:107; Csiki 1931:760; Blackwelder 1944:40.

This species is known definitely only from the type, but *P. rectilineus* may be conspecific.

*Platynus procephalus* (Bates), new combination.

*Colpodes procephalus* Bates 1878:597. Lectotype male, here designated, selected by G. E. Ball, "Guatemala", "*Colpodes procephalus* Bates" (Bates, MNHP).

*Colpodes procephalus*, Bates 1882:106; Csiki 1931:760; Blackwelder 1944:40.

*Colpodes procephalus* var. *hondurae* Bates 1882:106. Holotype female, *Colpodes hondurae* Bates", labelled as holotype by G. E. Ball 1972 (BMNH). New synonymy.

*Colpodes procephalus hondurae*, Csiki 1931:760; Blackwelder 1944:40.

In Mexico, this species is known only from extreme southeastern Chiapas. This species is strongly but continuously geographically varied; apices of male genitalia are not varied, but differ markedly from those of *P. championi*, a species which is closely related, sympatric, and similarly varied.

*Platynus profundus* (Barr), new combination.

*Mexisphodrus profundus* Barr 1966:113; holotype in MCZ. See Barr (1966) for description and comparison with related species; I doubt, however, that either this or "*Mexisphodrus*" *tlaymayensis* are closely related to *P. veraecrucis*, type species of *Mexisphodrus*.

[*Platynus prolongatus* (Bates), see *P. cycloderus* (Chaudoir)].

*Platynus pterostichoides* (Bates), new combination.

*Colpodes pterostichoides* Bates 1882:102. Lectotype male, here designated, "Las Vigas, Mexico, Hoege" (BMNH).

*Colpodes pterostichoides*, Csiki 1931:760; Blackwelder 1944:40.

This species is known from various localities in the states of Oaxaca and Veracruz, as cited by Bates (1882). The taxonomic relationships and status of this species are unclear.

[*Platynus punctatostriatus* (Chaudoir), see *P. niger* (Chaudoir)].

*Platynus purpuratus* (Reiche), new combination.

*Dyscolus purpuratus* Reiche 1842:375. Lectotype female, here designated, "purpuratus Rev. Zool. 1842 p. 375", "Ex Musaeo Chaudoir" (MNHP, 296/1/3). Type locality "Novae-Granatae".

*Colpodes purpuratus*, Chaudoir 1878:340; Bates 1882:118; Csiki 1931:761; Blackwelder 1944:40.

*Dyscolus chalcopertus* Reiche 1842:375. Lectotype female, here designated, "Columbia Lebas", "Ex Musaeo Chaudoir" (MNHP, 296/1/3). Type locality "Novae-Granatae". Synonymy by Chaudoir (1878).

*Colpodes chalcopertus*, Chaudoir 1859:340.

If my interpretation of this species is accurate, *P. purpuratus* ranges from Chiapas to Colombia.

*Platynus purulensis* (Bates), new combination.

*Colpodes purulensis* Bates 1882:110. Lectotype male, here designated, "TYPE H.T.", "Purula Guatemala Champion" (BMNH); male and female pinned together.

*Colpodes purulensis*, Csiki 1931:761; Blackwelder 1944:40.

I regard specimens from various localities in Chiapas as conspecific with Guatemalan specimens of *P. purulensis*, but they differ by having shallower elytral striae and less convex elytral intervals.

*Platynus quadrilaterus* (Bates), new combination.

*Colpodes quadrilaterus* Bates 1882:128. Lectotype male, here designated, "TYPE H.T.", "Jalapa, Mexico Höge" (BMNH).

*Colpodes quadrilaterus*, Csiki 1931:761; Blackwelder 1944:40.

In addition to records from Jalapa and Mexico City (Bates, 1882), I have examined specimens from Fortin de las Flores, Veracruz, Mexico. This species is closely related to *P. iricolor*.

[*Platynus recticollis* (Casey), see *P. rectilineus* (Bates)].

*Platynus rectilineus* (Bates), new combination.

*Colpodes rectilineus* Bates 1891:257. Lectotype female, here designated, "TYPE H. T.", "Omilteme ..." (BMNH)

*Colpodes rectilineus*, Csiki 1931:761; Blackwelder 1944:40.

*Anacolpodes recticollis* Casey 1920:18. Holotype male, "Guer.", "TYPE USNM 47391" (USNM). New synonymy.

*Colpodes recticollis*, Csiki 1931:761; Blackwelder 1944:40.

This species is related to and perhaps conspecific with *P. pristonychoides*. It is known only from the vicinity of Omilteme, Guerrero, Mexico.

*Platynus reflexicollis* (Chaudoir), new combination.

*Colpodes reflexicollis* Chaudoir 1859:328. Holotype female, "130", "Ex Musaeo Chaudoir" (MNHP, 296/5/2). Type locality near "pic d'Orizaba", Veracruz, Mexico.

*Colpodes reflexicollis*, Chaudoir 1878:353; Bates 1882:124; Csiki 1931:761; Blackwelder 1944:40.

This species is known only from the state of Veracruz.

*Platynus reflexus* (Chaudoir), new combination.

*Colpodes reflexus* Chaudoir 1859:347. Holotype male, "Ex Musaeo Chaudoir" (MNHP, 296/6/5). Type locality near "Cordova", Veracruz, Mexico.

*Colpodes reflexus*, Chaudoir 1878:358; Bates 1882:125; Csiki 1931:761; Blackwelder 1944:40.

This species is known only from the type specimen.

*Platynus robustus* (Chaudoir), new combination.

*Colpodes robustus* Chaudoir 1878:296. Holotype male, "Mexique", "Soc. Ent. Belg. Coll. Putzeys" (IRSB). Type locality "Mexique".

*Colpodes robustus*, Bates 1882:103; Csiki 1931:761; Blackwelder 1944:40.

This distinctive species is known from several localities in the state of Chiapas.

*Platynus (Rhadine) rotgeri* Bolivar and Hendrichs, new combination.

See Bolivar and Hendrichs, 1964.

*Platynus rubidus* (Chaudoir, new combination.

*Colpodes rubidus* Chaudoir 1878:329. Lectotype male, here designated, darker of two males labelled "Ex Musaeo Chaudoir" (MNHP. 295/5/1). Type locality "Oaxaca", Mexico.

*Colpodes rubidus*, Bates 1882:113; Csiki 1931:761; Blackwelder 1944:40.

This species was reported from Juquila, Oaxaca, Mexico by Bates (1882); I have seen no fresh material.

*Platynus ruficornis* (Chaudoir), new combination.

*Colpodes ruficornis* Chaudoir 1859:346. Lectotype male, here designated, "Ex Musaeo Chaudoir" (MNHP, 296/6/6). Type locality "Cordova", Veracruz, Mexico.

*Colpodes ruficornis*, Chaudoir 1878:358; Bates 1882:125; Csiki 1931:762; Blackwelder 1944:40.

This species is known from various localities in Veracruz, but its real taxonomic status and relationships are uncertain.

*Platynus rufiventris* (Van Dyke), new combination.

*Colpodes rufiventris* Van Dyke 1926:120. Holotype male, "Nogales Ariz J. A. Kusche July 1919-10", "6000 ft Mt. Washington", "Van Dyke Collection" (CAS).

*Colpodes rufiventris*, Csiki 1931:762; Leng and Mutchler 1933:13.

This species, known from several localities in southern Arizona, is a member of a poorly understood complex which is widespread in Mexico.

[*Platynus rufulus* (Bates), new combination].

*Colpodes rufulus* Bates 1884:286. Holotype male, "TYPE H.T.", "Sp. figured", "Tocoy, Verapaz, Champion", "BCA Col. I. 1., *Colpodes rufulus* Bates", "*Colpodes rufulus* Bates", "HOLOTYPE" (disc), "ind. G. E. Ball '72" (BMNH).

*Colpodes rufulus*, Csiki 1931:762; Blackwelder 1944:40

This species, which is not yet known from Mexico, is of uncertain relationships it may be related to *P. colibor*, or may be a component of the *ovatulus* complex. G. E. Ball (*in. litt.*) notes that it will most easily key near *P. macrourus*, and that its body length is nearer 10 mm than 7 mm as characteristic of members of the *ovatulus* complex in general.

*Platynus scabricollis* (Bates), new combination.

*Colpodes scabricollis* Bates 1882:126. Lectotype male, here designated, "TYPE H.T.", "Cerro Zunil 4000 ft. Champion" (BMNH). Type locality Cerro Zunil, Guatemala.

*Colpodes scabricollis*, Csiki 1931:762; Blackwelder 1944:40.

The only known Mexican locality for this otherwise Central American species is in the state of Veracruz.

*Platynus segregatus* (Bates), new combination.

*Colpodes segregatus* Bates 1891:258. Lectotype female, here designated, "TYPE H.T.", "Cuernavaca, Morelos. Höge", "Sp. figured", "Tr. Ent. S. L. 1891 *Colpodes segregatus*, Bates" (BMNH).

*Colpodes segregatus*, Csiki 1931:762; Blackwelder 1944:40.

I have examined specimens of this species, a close relative of *P. falli*, from the states of Colima, Guerrero, Michoacan, Morelos, and Oaxaca.

*Platynus semiopacus* (Chaudoir), new combination.

*Colpodes semiopacus* Chaudoir 1878:322. Lectotype female, here designated, female with both hind legs intact, "Ex Musaeo Chaudoir" (MNHP, 295/2/4). Type locality "Oaxaca", Mexico.

*Colpodes semiopacus*, Bates 1882:106; Csiki 1931:762; Blackwelder 1944:40.

This species, closely related to and perhaps conspecific with *P. biovatus*, is known from various localities in the state of Oaxaca.

*Platynus severus* (Chaudoir), new combination.

*Colpodes severus* Chaudoir 1878:321. Holotype male, "Chiapas 5-7-58", "Soc. Ent. Belg. Coll. Putzeys", "C. severus Chaud" (Chaudoir script) (IRSB).

*Colpodes severus*, Bates 1882:107; Csiki 1931:762; Blackwelder 1944:40.

This species is known from various upland localities in the state of Chiapas.

*Platynus sexfoveolatus* (Chaudoir), new combination.

*Colpodes sexfoveolatus* Chaudoir 1878:332. Lectotype female, here designated, "cum diluto confusus", "Ex Musaeo Chaudoir" (MNHP, 295/5/1). Type locality "Mexique".

*Colpodes sexfoveolatus*, Bates 1882:115; Csiki 1931:762; Blackwelder 1944:40.

Specimens examined from various localities in Chiapas are most probably conspecific with the type, but the taxonomic status and relations of this species are uncertain.

[*Platynus sexpunctatus* (Chaudoir), see *P. chaudoiri* (Coquerel)].

[*Platynus simplicior* (Bates), see *P. nugax* (Bates)].

*Platynus sphodroides* (Chaudoir), new combination.

*Colpodes sphodroides* Chaudoir 1859:309. Lectotype male, here designated, third specimen labelled "Ex Musaeo Chaudoir" (MNHP, 295/2/3). Type locality "Parada", Oaxaca, Mexico.

*Colpodes sphodroides*, Chaudoir 1878:322; Bates 1882:109; Csiki 1931:763; Blackwelder 1944:40.

This species is known from several localities in the state of Oaxaca.

*Platynus spinifer* (Bates), new combination.

*Colpodes spinifer* Bates 1882:116. Lectotype female, here designated, "TYPE H.T.", "Cerro Zunil 4000 ft. Champion" (BMNH). Type locality Cerro Zunil, Guatemala.

*Colpodes spinifer*, Csiki 1931:763; Blackwelder 1944:40.

This Central American species is known in Mexico only from extreme southeastern Chiapas.

[*Platynus stenos* (Bates), see *P. nitidus* (Chaudoir)].

*Platynus steropoides* (Bates), new combination.

*Colpodes steropoides* Bates 1891:254. Lectotype male, here designated, "Omiteme Guerrero 8000 ft. Aug. H. H. Smith", "Sp. figured" (BMNH).

*Colpodes steropoides*, Csiki 1931:763; Blackwelder 1944:40.

This species is known only from the type locality, state of Guerrero.

*Platynus striatopunctatus* (Chaudoir), new combination.

*Colpodes striatopunctatus* Chaudoir 1859:332. Holotype female, "Ex Musaeo Chaudoir" (MNHP, 295/3/7). Type locality "Toxpam", Veracruz, Mexico.

*Colpodes striatopunctatus*, Chaudoir 1878:329; Bates 1882:113; Csiki 1931:763; Blackwelder 1944:40.

This species is known from various localities in the state of Veracruz.

*Platynus stricticollis* (Bates), new combination.

*Colpodes stricticollis* Bates 1878:575. Lectotype female, here designated, "Chontales" (Bates, MNHP). Type locality Chontales, Nicaragua.

*Colpodes stricticollis*, Bates 1882:102; Csiki 1931:763; Blackwelder 1944:40.

This species is widespread in the tropical lowlands of Mexico and Central America; it is not closely related to other known species.

*Platynus subauratus* (Bates), new combination.

*Colpodes subauratus* Bates 1882:113. Lectotype male, here designated, "TYPE H.T.", "Jalapa, Mexico. Hoege" (BMNH).

*Colpodes subauratus*, Csiki 1931:763; Blackwelder 1944:40.

This species is known from various localities in the states of Puebla and Veracruz.

*Platynus subcyaneus* (Chaudoir), new combination.

*Colpodes subcyaneus* Chaudoir 1878:339. Lectotype female, here designated, "Mexique", "A. Deyrolle", "Ex Musaeo Chaudoir" (MNHP, 295/6/6). Type locality "Mexique".

*Colpodes subcyaneus*, Bates 1882:118; Csiki 1931:763; Blackwelder 1944:40.

The taxonomic status of this form is uncertain; it may be a component of *P. aequinoctialis*. I tentatively place as this species specimens from various localities in the states of Oaxaca, Puebla, and Veracruz.

[*Platynus suffectus* (Bates), see *P. concisus* (Bates)].

[*Platynus tenuicollis* (LeConte)].

See Lindroth (1966) for synonymic and other details about *P. tenuicollis* LeConte 1848

I add the following.

*Colpodes approximatus* Chaudoir 1878:370. Holotype female, "Ex Musaeo Chaudoir" (MNHP, 297/3/8). Type locality originally given as "nord du Mexique"; I here translate this as "(in the) north of Mexico", but prior to cession of regions north of the Rio Grande to the United States; and I here restrict the type locality to Jefferson County, Colorado, United States. New synonymy.

*Colpodes approximatus*, Bates 1882:129; Csiki 1931:748; Blackwelder 1944:37.

This species is incorrectly listed as from Mexico. I have examined 17 specimens from various localities in Jefferson County, Colorado (in collection of D. H. Kavanaugh); these are of the western form of *P. tenuicollis* which is distinguished by flattened form, pale legs, and other details; and this is the form represented by the type specimens of both *tenuicollis* LeConte and *approximatus* Chaudoir. Chaudoir (1878) correctly indicated relationship with *P. marginatus* LeConte 1848, now known to be the eastern form of *P. tenuicollis* and characterized by convex form and dark legs. Geographic variation in this phylogenetically rather isolated species is complex and in need of detailed study.

*Platynus tenuicornis* (Chaudoir), new combination.

*Colpodes tenuicornis* Chaudoir 1859:333. Lectotype male, here designated, first male in first of two rows labelled "Ex Musaeo Chaudoir" (MNHP, 295/4/5). Type locality near "Cordova", Veracruz, Mexico.

*Colpodes tenuicornis*, Chaudoir 1878:331; Bates 1882:114; Csiki 1931:764; Blackwelder 1944:40.

This species is known only from several localities in the vicinity of Cordova, Jalapa, and Orizaba in the state of Veracruz. Records from other localities (Bates, 1882) pertain to *P. cycloderus*.

*Platynus teter* (Chaudoir), new combination.

*Colpodes teter* Chaudoir 1878:321. Lectotype male, here designated, "Mexique", "Soc. Ent. Belg. Coll. Putzeys" (IRSB); the "Mexique" label is not Putzeys' original label, and the specimen lacks Chaudoir's determination label. A female, same collection, bears the label. "Chiapas 5-7-58" and is the second of two original specimens. Type locality state of Chiapas, Mexico.

*Colpodes teter*, Bates 1882:107; Csiki 1931:764; Blackwelder 1944:40.

This species is known from several upland localities in the state of Chiapas.

*Platynus tlamayensis* (Barr), new combination.

See Barr (1966) for description and other information.

*Platynus (Platynella) tolucensis* (Straneo), new combination.

See Barr (1970) for further information.

*Platynus transfuga* (Chaudoir), new combination.

*Colpodes transfuga* Chaudoir 1878:297. Lectotype male, here designated, "Type", "Parada", "Mexico. Salle Coll." (BMNH). Type locality Parada, Oaxaca, Mexico.

*Colpodes transfuga*, Bates 1882:103; Csiki 1931:764; Blackwelder 1944:40

This species is known from various localities in Oaxaca.



*Platynus transversicollis* (Chaudoir), new combination.

*Colpodes transversicollis* Chaudoir 1859:343. Holotype female, "Ex Musaeo Chaudoir" (MNHP, 296/4/4). Type locality "Mexique".

*Colpodes transversicollis*, Chaudoir 1878:350; Bates 1882:123; Csiki 1931:764; Blackwelder 1944:40.

*Colpodes unilobatus* Bates 1882:117. Lectotype male, here designated, "TYPE H.T.", "Cerro Zunil 4000 ft. Champion" (BMNH). Type locality Cerro Zunil, Guatemala. New synonymy.

*Colpodes unilobatus*, Csiki 1931:764; Blackwelder 1944:40.

Known Mexican localities for this species are in the states of Chiapas and Veracruz.

[*Platynus tristis* (Chaudoir), see *P. moestus* (Dejean)].

[*Platynus trujilloi* (Bates), see *P. fratellus* (Chaudoir)].

*Platynus (Stenoplatynus) umbripennis* (Casey), new combination.

*Hemiplatynus (Stenoplatynus) umbripennis* Casey 1920:17. Holotype in USNM. See Barr *et al.* (1968).

*Agonum umbripenne*, Ciskii 1931:849 (subgenus *Hemiplatynus*); Blackwelder 1944:42; Barr *et al.* 1968:107 (subgenus *Platynus*).

*Agonum (Platynus) bilimeki* Bolivar and Hendrichs 1965:226. See Bolivar and Hendrichs (1965) for description and details.

This species is known from limestone areas on south-facing slopes of the Transvolcanic Sierra of central Mexico. See papers by Bolivar and Hendrichs (1965) and Barr *et al.* (1968) for descriptions of adult and larva, and for notes on synonymy.

[*Platynus unilobatus* (Bates), see *P. transversicollis* (Chaudoir)].

*Platynus valens* (Bates), new combination.

*Colpodes valens* Bates 1891:255. Lectotype male, here designated, "Ciudad, Durango. Höge", "Sp. figured" (BMNH).

*Colpodes valens*, Csiki 1931:764; Blackwelder 1944:40.

This species, known from various high elevation localities in Durango, Mexico, is similar to *P. durangensis* but is sympatric and doubtless distinct.

*Platynus validus* (Chaudoir), new combination.

*Colpodes validus* Chaudoir 1859:342. Lectotype female, here designated, specimen with left hind tarsus and labelled "Ex Musaeo Chaudoir" (MNHP, 296/1/2). Type locality "Orizaba", Veracruz, Mexico.

*Colpodes validus*, Chaudoir 1878:340; Bates 1882:119; Csiki 1931:764; Blackwelder 1944:40.

This species is known definitely only from the two original female specimens. Records cited by Bates (1882) may pertain to *P. variabilis*; indeed, *P. validus* and *P. variabilis* may not be reproductive isolates.

*Platynus variabilis* (Chaudoir), new combination.

*Dyscolus variabilis* Chaudoir 1837:15. Lectotype male, here designated, "Variabilis Chevrolat Mexico D. Chevrolat", "Ex Musaeo Chaudoir" (MNHP, 296/1/4). Type locality "Mexico".

*Colpodes variabilis*, Chaudoir 1859:340; Chaudoir 1878:340; Bates 1882:119; Csiki 1931:764; Blackwelder 1944:40.

*Anchomenus (Plocodes) guerrensis* Casey 1920:28. Holotype female, "Guer", "TYPE USNM 47398" (USNM). New synonymy.

*Colpodes guerrensis*, Csiki 1931:754; Blackwelder 1944:39.

This species is widespread in Mexico, from Tamaulipas and Jalisco south to Oaxaca.

*Platynus (Mexisphodrus) veraecrucis* (Barr), new combination.

*Mexisphodrus veraecrucis* Barr 1965:66. Holotype in MCZ; see Barr (1965, 1966) for further information.

[*Platynus versicolor* (Motschoulsky), see *P. cycloderus* (Chaudoir)].

*Platynus violaceipennis* (Chaudoir), new combination.

*Colpodes violaceipennis* Chaudoir 1859:340. Lectotype male, here designated, "145", "Ex Musaeo Chaudoir" (MNHP, 296/1/6). Type locality "Orizaba", Veracruz, Mexico.

*Colpodes violaceipennis*, Chaudoir 1878:340; Bates 1882:119; Csiki 1931:765; Blackwelder 1944:40.

I did not confirm records cited by Bates (1882), and have no new records to add.

## DISCUSSION

This work should not be used, save with great caution, to attempt identifications of Central American specimens of *Platynus* (or "*Colpodes*"). And, though I developed this paper to fully distinguish all *described* Mexican species— the key is extracted from a manuscript key to all forms known to me— some, especially localized flightless forms, may not be adequately distinguished from undescribed forms not yet known to me. I have seen representatives of about 100 undescribed forms which probably are distinct from the 125 described species here recognized. Further, I estimate that the Mexican *Platynus* fauna, when fully documented, will include some 300 to 500 species, probably over 400. Especially poorly known at present are flightless inhabitants of isolated cloud forests; the faunas of even some of the highest southern mountains, such as Volcan Tacaná in southern Chiapas, remain totally unknown.

More than 20% of names already proposed for the still barely known Mexican *Platynus* fauna are synonyms. Clearly, if additional names are heedlessly proposed, synonyms will increase in number and percentage. Thus, I hope my work will not encourage production of isolated new descriptions; rather, I hope it will serve as background for careful analyses of groups of related species. Delineation and definition of such groups are much needed. My key may indirectly suggest some such groupings, and some already available genus— group names such as *Rhadine*, *Stenocnemus*, *Ophryodactylus*, and *Platynella* may well be applied to groups of subgeneric rank, but all such groups first need to be better defined.

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STUDIES ON BOREAL AGROMYZIDAE (DIPTERA), IV.  
PHYTOMYZA MINERS ON ANGELICA, HERACLEUM,  
LASERPITIUM AND PASTINACA (UMBELLIFERAE)

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*Nine species of the Phytomyza albiceps group and five of the Phytomyza angelicae group are recorded as miners of Angelica, Heracleum, Laserpitium and Pastinaca. These include one new species on Heracleum, P. tlingitica n. sp. (type-locality Chilkat peninsula, Alaska). The identity of P. spondylii Robineau-Desvoidy is clarified. P. archangelicae Hering and P. angelicae Kaltenbach are recorded for the first time in North America; and the North American P. heracleiphaga Spencer is considered a subspecies of the true P. spondylii Robineau-Desvoidy. Two names are newly synonymized, P. angelicella Frost (= P. pastinacae Hendel) and P. laserpitii Hendel (= P. angelicae Kaltenbach). P. kibunensis Sasakawa, described as a subspecies of angelicae, is considered a full species.*

*Neuf espèces du groupe Phytomyza albiceps et cinq espèces du groupe Phytomyza angelicae sont signalées comme mineuses de l'Angelica, de l'Heracleum, du Laserpitium et de la Pastinaca. Une espèce nouvelle est incluse, P. tlingitica n. sp. sur l'Heracleum (localité-type Péninsule de Chilkat, Alaska). L'identité de P. spondylii Robineau-Desvoidy est clarifié. P. archangelicae Hering et P. angelicae Kaltenbach sont signalées pour la première fois en Amérique du nord; et P. heracleiphaga Spencer d'Amérique du nord est considérée comme sous-espèce de la vraie P. spondylii Robineau-Desvoidy. Deux noms sont de nouveau synonymisés, P. angelicella Frost (= P. pastinacae Hendel) et P. laserpitii Hendel (= P. angelicae Kaltenbach). P. kibunensis Sasakawa, décrite comme sous-espèce d'angelicae, est considérée comme espèce proprement dite.*

*Neun Arten der Phytomyza albiceps-Gruppe und fünf Arten der Phytomyza angelicae-Gruppe werden als Minierer von Angelica, Heracleum, Laserpitium und Pastinaca besprochen. Unter diesen wird eine Art an Heracleum, P. tlingitica n. sp. (Fundort vom Typus Chilkathalbinsel, Alaska) neu beschrieben. Die Identität von P. spondylii Robineau-Desvoidy wird geklärt. P. archangelicae Hering und P. angelicae Kaltenbach werden zum ersten Mal für Nordamerika nachgewiesen; die nordamerikanische P. heracleiphaga Spencer wird als Unterart der echten P. spondylii Robineau-Desvoidy angesehen. Zwei Namen werden neu synonymisiert: P. angelicella Frost (= P. pastinacae Hendel) und P. laserpitii Hendel (= P. angelicae Kaltenbach). P. kibunensis Sasakawa, als Unterart von angelicae beschrieben, wird als volle Art angesehen.*

The present paper deals with all known *Phytomyza* miners of four genera of Umbelliferae, *Angelica*, *Heracleum*, *Laserpitium* and *Pastinaca*. These belong to two groups, the *albiceps* group and the *angelicae* group.

The terms and abbreviations used in my descriptions were explained in the first paper of this series (Griffiths, 1972a). Names of North American plants are used in the sense of

Hultén (1968), and of European plants in the sense of Tutin (1968). Following the latter the names *Heracleum sphondylium* L. and *Angelica archangelica* L. are here used in wide senses, including subspecies which have been listed as full species in some previous host-plant records. Japanese plants are listed in the form used by Sasakawa (1961a, 1961b).

The holotype of the new species described in this paper will be deposited in the Canadian National Collection (Ottawa).

## DIAGNOSIS

Keys with worldwide coverage to the mines of *Phytomyza* species on *Angelica*, *Heracleum*, *Pastinaca* and *Laserpitium* are given below. The only other agromyzid species recorded as a leaf-miner on these plant genera is the polyphagous *Liriomyza strigata* Meigen, recorded (rarely) on *Heracleum* in Europe by Hering (1957:524). The larvae of this species feed mainly in the leaf midrib, producing mines very distinct from those of the *Phytomyza* species here treated. Larvae of two other *Liriomyza* species (*L. lutea* Meigen and *L. wachtl*i Hendel) are known to feed on the seeds, and those of *Napomyza carotae* Spencer and several *Melanagromyza* and *Ophiomyia* species in the stems.

The species of *Phytomyza* treated in this paper belong to critical groups, in which the male aedeagus must be studied for reliable identification. Some cannot be separated on the basis of their mines and larvae. Amendments to Spencer's (1969) key to the *Phytomyza* species of Canada and Alaska to incorporate additional species are as follows. These expand amendments already proposed by Sehgal (1971) and in my previous paper (Griffiths, 1973).

- 13. Upper ors shorter than lower or lacking . . . . . 13a
- Both ors equal . . . . . 14
- 13a. Third antennal segment with conspicuously long pubescence; aedeagus as Sehgal's Fig. 121 . . . . . *riparia* Sehgal
- Third antennal segment with short pubescence . . . . . 13b
- 13b. Sutural triangle entirely whitish; humeral callus partly so (infuscated only at centre). Aedeagus as Figs. 8, 9 . . . . . *tingitica* n. sp.
- Sides of mesonotum with less pale coloration (at most on upper part of sutural triangle and at corners of humeral callus). . . . . 13c
- 13c. Aedeagus as Figs. 5, 6 . . . . . *spondylii heracleiphaga* Spencer
- Aedeagus as Figs. 2, 3 . . . . . *pastinacae* Hendel
  
- 84. Tarsi yellow; aedeagus as Spencer's Figs. 402, 403 . . . . . *aralivora* Spencer
- Tarsi dark . . . . . 84a
- 84a. Distal section of aedeagus long. . . . . 84b
- Distal section of aedeagus very short . . . . . 84c
- 84b. Basal section of aedeagus with two rows of conspicuous spinules (Griffiths, 1973, Fig. 7). . . . . *sitchensis* Griffiths
- Basal section of aedeagus without spinules (Spencer's Figs. 473, 474). . . . . *osmorhizae* Spencer
- 84c. Aedeagus as Figs. 17, 18, with medial lobe scarcely differentiated . . . . . *archangelicae* Hering
- Medial lobe of aedeagus well differentiated, with left sclerite expanded (Griffiths, 1973, Figs. 4, 5). . . . . *conioselini* Griffiths



Key to *Phytomyza* mines on *Angelica*

1. Anal lobes of puparium prominent . . . . . 2
- Anal lobes of puparium not prominent . . . . . 3
2. Mine (Fig. 43) primary blotch, without initial linear channel, normally communal (produced by more than one larva). Holarctic . . . . . *P. angelicae* Kaltenbach
- Mine primarily linear, with irregular blotchy areas terminally, produced by single larva. Japan . . . . . *P. kibunensis* Sasakawa
3. Mine entirely on upper surface of leaf (without initial channel on lower surface), linear throughout . . . . . 4
- Mine with short initial channel on lower surface of leaf, linear throughout or with blotchy areas . . . . . 5
4. Posterior spiracles of puparium and third instar larva with slender horns (Sasakawa, 1955, Fig. 7b). Japan . . . . . *P. polycladae* Sasakawa
- Posterior spiracles of puparium and third instar larva without distinct horns. Holarctic . . . . . *P. pastinacae* Hendel
5. Puparia very small, 1.5-1.6 mm long. Mine becoming blotchy terminally, following leaf margin. Eastern Europe. On *Angelica palustris* (Besser) . . . . . *P. angelicivora* Hering
- Puparia normally larger. On other *Angelica* species . . . . . 6
6. Mine (Fig. 42) linear throughout; posterior spiracles of puparium and third instar larva with 20-28 bulbs (Fig. 39). Holarctic . . . . . *P. archangelicae* Hering
- Mine basically linear, but normally convolute, with secondarily blotchy areas (Fig. 41) . . . . . 7
7. Posterior spiracles of puparium and third instar larva with 30-35 bulbs. Japan. . . . . *P. arnaudi* Sasakawa
- Posterior spiracles of puparium and third instar larva with 22-28 bulbs (Fig. 37). Europe . . . . . *P. angelicatri* Hering

Key to *Phytomyza* mines on *Heracleum* and *Pastinaca*

1. Anal lobes of puparium prominent. Mine primary blotch . . . . . 2
- Anal lobes of puparium not prominent. Mine basically linear, although with blotchy areas in some species . . . . . 3
2. Mine (Fig. 44) interparenchymal throughout, with marbled appearance caused by scattered holes eaten in palisade parenchyma, produced by single larva. Europe . . . . . *P. heracleana* Hering
- Mine (Fig. 43) largely of uniform depth on upper surface of leaf, with only limited area of interparenchymal feeding (by first-instar larvae), normally communal (produced by more than one larva). Holarctic . . . . . *P. angelicae* Kaltenbach
3. Mine interparenchymal (pale green when fresh), basically linear but in most cases with blotchy areas (Fig. 40B) . . . . . 4
- Mine on upper surface of leaf (whitish when fresh), linear throughout (Fig. 40A). . . . . 5
4. Europe . . . . . *P. sphondyliivora* Spencer
- Alaska . . . . . *P. tlingitica* n. sp.
5. Europe . . . . . *P. spondylii spondylii* Robineau-Desvoidy  
or *P. pastinacae* Hendel

- North America. . . . . *P. spondylii heracleiphaga* Spencer  
 . . . . . or *P. pastinacae* Hendel  
 . . . . . or *P. lanati* Spencer

#### Key to *Phytomyza* mines on *Laserpitium*

1. Mine primary blotch, without initial linear channel, normally communal (produced by more than one larva) . . . . . *P. angelicae* Kaltenbach  
 — Mine linear, produced by single larva . . . . . *P. latifolii* Groschke

### TREATMENT OF SPECIES

#### (a) the *Phytomyza albiceps* group

See my previous discussion of this group (Griffiths, 1972b). Nowakowski (1926: 105) has discussed the relationships of the Umbelliferae-feeding members of this group. Six of the species here treated belong to Nowakowski's "fourth subgroup", which I propose to call the *spondylii* subgroup. These are yellow-fronted species characterized by a large but mostly unpigmented distal section of the aedeagus without paramesophalli. I refer to this subgroup the following species treated in this paper: *P. spondylii* Robineau-Desvoidy, *P. pastinacae* Hendel, *P. sphondyliivora* Spencer, *P. tlingitica* n. sp., *P. angelicastris* Hering and *P. lanati* Spencer. Other species known to belong to this subgroup are *P. sii* Hering (Nowakowski, 1962), *P. cicutae* Hendel (Nowakowski, 1962), *P. conii* Hering (Spencer, 1971) and *P. oen-anthes* Sasakawa. All species of this subgroup are very similar, and study of the male aedeagus is usually necessary for identification.

In addition to species of the *spondylii* subgroup, two dark-fronted species with highly modified aedeagus, *P. archangelicae* Hering and *P. arnaudi* Sasakawa, also occur on *Angelica*. Their affinities doubtless lie with some of the dark-fronted species of the *albiceps* group on other genera of Umbelliferae; but too few of these have been critically studied to define a subgroup at this time.

The relationships of *P. polycladae* Sasakawa cannot be determined until males are obtained from the original host-plant. My listing of this species under the *albiceps* group is only provisional.

Nowakowski (1962: 105) has included *P. angelicae* Kaltenbach and its relatives (among which I also include *P. heracleana* Hering) as a subgroup of the *albiceps* group. I am doubtful whether this is correct, and treat the *angelicae* group separately below.

#### *Phytomyza spondylii* Robineau-Desvoidy 1851

(synonymy below under subspecies)

*Adult*. — Head with orbits narrowly projecting above eye in lateral view; genae in middle 1/3 to 1/2 of eye height; eyes with only sparse fine pubescence. Frons at level of front ocellus about twice width of eye. Ors directed posteriorly, ori directed inwardly; posterior ors variably developed, ranging from only slightly shorter than anterior ors to completely absent (short in most specimens); anterior ori short or absent, at most half as long as posterior ori; orbital setulae numerous, irregularly distributed, more or less two-rowed posteriorly. Peristomal margin with vibrissa and 4-6 upcurved peristomal setulae. Third antennal article rounded distally, with short white pubescence.

3 + 1 dc; acr in 3-4 irregular rows; 5-12 presutural ia; 4-8 postsutural ia; inner pa 1/2 to 2/3 as long as outer pa.

Second cross-vein (m-m) absent. Costal ratio  $mg_2/mg_4$  3.4-4.8 (mean 3.85).

Centre of frons clear yellow, contrasting with dark ocellar plate and vertex (both vt on dark ground); orbits partly infuscated (at least along eye margins and around bases of orbital setae; in some specimens broadly infuscated from eye margin to level of orbital setae). Face largely infuscated. Genae yellow. Occiput dark. Antennae with first article yellow-brown or brown, second and third articles dark brown to black. Palpi dark brown; labella yellow or white. Mesonotum weakly shining, finely grey-dusted, largely dark but with patches of brown or yellow-brown coloration on sides (especially at corners of humeral callus and on upper part of sutural triangle); scutellum dark; mesopleuron largely dark, with whitish dorsal band (very narrow in most specimens, at most 1/4 of height of mesopleuron); other pleura largely dark, but with some pale coloration along sutures. Wing base and squamae whitish, latter with contrastingly dark fringe. Legs largely dark, with tips of front femora contrastingly yellow; tips of other femora less contrasting, yellow-brown to reddish. Abdomen largely brown. Basal cone of ovipositor (♀) grey dusted on basal third to half.

Male postabdomen with 8th sternum fused with 6th tergum. Telomeres not clearly delimited from perianthrium, bearing dense group of setulae. Pregonites weakly pigmented, extending ventrally (shielding base of aedeagus at rest). Aedeagal hood with two pairs of lateral sclerites (the more dorsal pair rather ill-defined). Aedeagus as Fig. 5, 6; 1-3 dorsal spinules on left side of basal section near apex of left basal sclerite; 0-6 similar dorsal spinules on right side near apex of right basal sclerite (see below under subspecies); main sclerites of medial lobe in some specimens fused to form loop (as in *pastinacae*), but more commonly separate distally, turned forward in many specimens (as in Fig. 5); additional short sclerite at left basal corner of medial lobe (in some specimens weakly spiniform); smaller more or less spiniform sclerite in similar position on right side; distal section long, without pigmented sclerites, with ventral notch or spinule (in most specimens with dark tip) on right side. Ejaculatory apodeme as Fig. 7.

*Puparium and third instar larva.* — Mandibles with two alternating teeth; right mandible longer than left. Anterior spiracles with two short horns, with 8-12 bulbs in widely open ellipse; posterior spiracles on short conical processes, with 18-21 bulbs in narrow ellipse. Puparia brown or black, 1.7 - 2.0 mm long, strongly arched, with intersegmental boundaries distinctly impressed; anal lobes not prominent.

*Mine.* — Larvae leaf-miners on *Heracleum* and *Pastinaca*. Mine (Fig. 40A) entirely linear, 6-10 cm long, 2-3 mm wide terminally; faeces deposited as fine particles, mostly separated by less than 1 mm, in some mines forming beaded strips on alternate sides of mine; mine formed entirely on upper surface of leaf, conspicuous, appearing white or greenish white in reflected light when fresh; larvae leaving leaf through semicircular slit on lower surface before puparium formation.

*Remarks.* — There are significant differences between European and North American material of this species in respect of size (for which wing length is here used as an indicator) and in the number of dorsal spinules on the right side of the aedeagus near the apex of the right basal sclerite (Fig. 1). Of course the available material does not demonstrate whether these differences are the result of discontinuous variation or a cline. Pending such clarification, I propose to regard the name proposed by Spencer (1969) for the North American populations as denoting a subspecies.

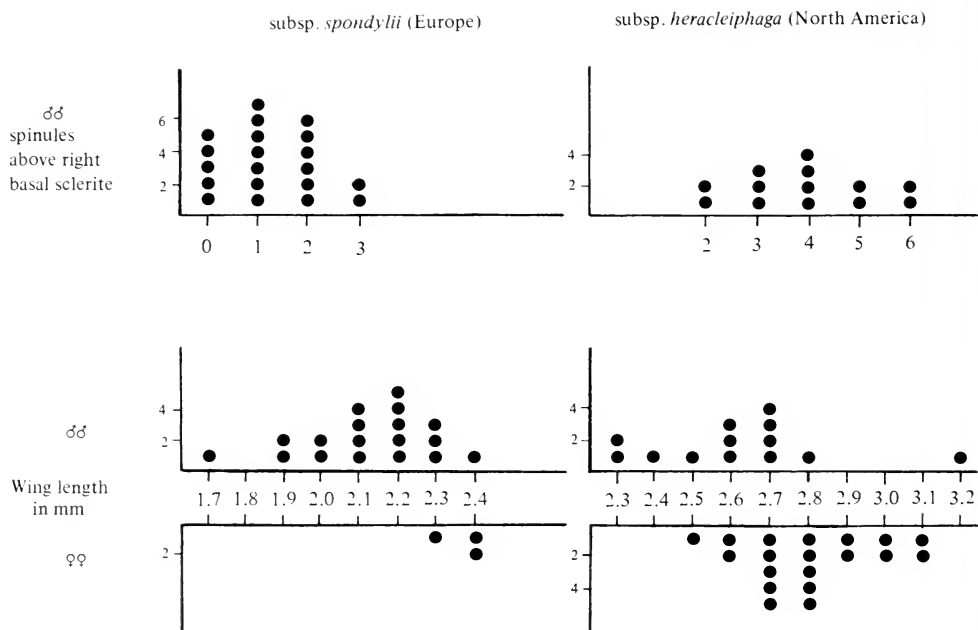


Fig. 1. Statistical differences between *Phytomyza spondylii spondylii* Robineau-Desvoidy and *P. s. heracleiphaga* Spencer, in respect of numbers of spinules near apex of right basal sclerite of aedeagus (♂) and wing length (♂♀). In addition to material examined, this figure includes information supplied in correspondence by von Tschirnhaus on 4♂♂ 1♀ *subsp. spondylii* and Spencer's (1969) data on the type series of *heracleiphaga*.

*Phytomyza spondylii spondylii* Robineau-Desvoidy 1851

"*Phytomyza nigra* Meigen". Goureau, 1851: 147.

*Phytomyza spondylii* Robineau-Desvoidy. Goureau, 1851: 147. Robineau-Desvoidy, 1851: 400. Hendel, 1935: 483 (as *sphondylii*). Lectotype ♂ by present designation, France, in University Museum, Oxford.

*Phytomyza heraclei* Kaltenbach. Kaltenbach, 1862: 33. — 1874: 284. Types lost; type-locality, Germany.

*Adult.* — Wing length 1.7-2.4 mm (Fig. 1). Aedeagus (♂) with 0-3 dorsal spinules on right side near apex of right basal sclerite (Fig. 1).

*Material examined.* — Lectotype ♂, 1♂ paratype bred by Goureau from *Heracleum sphondylium* L., France. 1♂ from Hendel collection (without data, presumably bred from *Heracleum sphondylium* L. in Austria). 3♂♂ from larvae on *Pastinaca sativa* L., Bredow bei Nauen, Germany, emerged 6-8.vii.23, leg. M. Hering (no. 2220). 1♂ from larva on *Heracleum sphondylium* L., Güntersberg an Oder, Germany, 1920, leg. M. Hering (no. 1325). 4♂♂ from larvae 22.v.66 on *Pastinaca sativa* L., Wittenberg, Germany, leg. K. H. Zoerner. 1♂ from larva 2.viii.56 on *Heracleum sphondylium* L., Berisal, Valais, Switzerland, emerged 23.viii.56, leg. K. A. Spencer. 1♂ (caught), Darenth, Kent, England, 9.v.54, leg. G. C. D. Griffiths. 1♂ 1♀ from larvae 15.viii.53 on *Heracleum sphondylium* L., Bookham, Surrey, England, emerged 4-5.ix.53, leg. G. C. D. Griffiths. 1♂ from larva 20.vi.54 on *Heracleum sphondylium* L., Betchworth, Surrey, emerged 14.vii.54, leg. G. C. D. Griffiths. 1♂ 1♀ from larvae

15.viii.54 on *Pastinaca sativa* L., Guildford, Surrey, emerged 4-6.ix.54, leg. G. C. D. Griffiths.

*Other records.* — Von Tschirnhaus (in correspondence) has supplied the following records, after study of my description and figures: 2♂♂ 1♀ from larvae 10.vii.70 on *Heracleum sphondylium* L., Borstel/Elbe, W of Hamburg, Niedersachsen, Germany, emerged 28.vii.70; 2♂♂ (caught), Kaiserstuhl/Rheintal, Baden-Württemberg, Germany.

*Remarks.* — Hendel's correction of the species name to "*sphondylii*" was unjustified according to the current rules of nomenclature, as the original spelling *spondylii* follows classical precedent and was not a lapsus. The name of the host-plant was in fact latinized as "spondylium" in Pliny's Natural History. Hering (Hering and Spencer, 1968: 220, 226) has also emphasized that Robineau-Desvoidy's original spelling was intentional.

Kaltenbach's name *heraclei* could equally well refer to this subspecies or to *pastinacae*. To avoid nomenclatural complications I follow Hendel in regarding the name as a synonym of *spondylii*.

Spencer (1969, 1971) has incorrectly applied the name *spondylii* to the species here called *pastinacae*. Following dissection of type material I am forced to change this interpretation. Until recently it was assumed that linear mines on *Heracleum* in Europe are all produced by a single monophagous species (*spondylii*), while those on *Pastinaca* are all produced by *pastinacae*. These names do in fact refer to different species, but both species occur on both these host plants. So the numerous records of these species in the European literature are in complete confusion, and we must start anew in attempting to assess their distribution. Thus the only reliable records of the true *spondylii* in Europe are those listed above. Hendel (1923, 1935) claimed to have found external differences between these species, but I cannot confirm them. As far as I can see, reliable diagnosis is only possible through study of the male aedeagus.

It is not known whether the descriptions of larvae and puparia given by de Meijere (1926, 1928, 1941) and Allen (1957) refer to this species or to *pastinacae*. Nowakowski (1962: 127) has figured the posterior larval spiracles of "*spondylii*" as having 15 bulbs, and those of "*pastinacae*" as having 25 bulbs. I can find no such distinction in the material before me, in which the number of bulbs on the posterior spiracles of *both* species lies between these numbers.

*Phytomyza spondylii heracleiphaga* Spencer 1969, new status

*Phytomyza heracleiphaga* Spencer. Spencer, 1969: 297. Holotype ♂, Berkeley Hills (California), in U. S. National Museum.

*Adult.* — Wing length 2.3-3.2 mm (Fig. 1). Aedeagus (♂) with 2-6 dorsal spinules on right side near apex of right basal sclerite (Fig. 1).

*Material examined.* — 12♂♂ 14♀♀ from larvae 26-30.vi.68 on *Heracleum lanatum* Michx., Chilkat peninsula (near Haines), Alaska, emerged 22-28.vii.68 (2♂♂ 1♀) and 3-8.v.69, leg. G. C. D. Griffiths.

*Other records.* — Spencer's (1969) description was based on 3♂♂ 5♀♀ bred by M. J. & C. A. Tauber from *Heracleum lanatum* Michx. at Strawberry Canyon, Berkeley Hills, California (emerged 27.iii-23.v.64). I have included data for these specimens on Fig. 1.

*Remarks.* — Spencer (1969: 251) suggests that the life-history information on "*lanati*" in papers by Tauber & Tauber (1966, 1968) in fact refers to *heracleiphaga*. I am not convinced of this, since those authors report the length of the leaf mines to be 25-29.5 cm, over twice as long as the mines produced by my Alaskan specimens. Additional studies are needed to clarify the distinction between mines of *heracleiphaga* and *lanati*.

*Phytomyza pastinacae* Hendel 1923

*Phytomyza pastinacae* Hendel. Hendel, 1923: 388.—1935: 449. Lectotype ♂ by present designation, Austria, in Naturhistorisches Museum, Vienna.

*Phytomyza angelicella* Frost. Frost, 1927: 218. Holotype ♂, Ithaca (New York), in U. S. National Museum, Washington. New synonymy.

"*Phytomyza spondylii* Robineau-Desvoidy". Spencer, 1969: 275.—1971: 187.

*Adult*. — As described for *spondylii*, except as follows.

3-4 upcurved peristomal setulae. Costal ratio  $mg_2/mg_4$  3.3-4.5 (mean 3.8). Wing length 2.0-2.5 mm.

Orbits infuscated along eye margins and around bases of orbital setae. Antennae with first article yellow-brown or brown, second article yellow-brown to dark brown, third article dark brown to black. Patches of pale coloration on sides of mesonotum variably developed, ranging from brown to contrastingly white. Basal cone of ovipositor (♀) grey dusted to variable extent, only narrowly at base on dorsal surface in Albertan specimens, on basal third to half in European specimens.

Aedeagus as Fig. 2, 3: conspicuous group of 6-11 dorsal spinules towards left side near apex of basal section; 1-5 similar dorsal spinules on right side near apex of right basal sclerite; medial lobe with asymmetrically oriented loop of sclerotization near left corner of which lies additional spiniform sclerite; no similar spiniform sclerite on right side (contrast *spondylii*); distal section without ventral notch, with small pigmented mesophallus differentiated near its base. Ejaculatory apodeme as Fig. 4.

*Puparium and third instar larva*. — Similar to those of *spondylii*. Posterior spiracles with 17-22 bulbs. Puparia 1.5-1.9 mm long.

*Mine*. — Larvae leaf-miners on *Pastinaca*, *Heracleum* and *Angelica*, forming linear upper-surface mines 6-9 cm long; otherwise as described for *spondylii*.

*Material examined*. — Lectotype ♂ from larva on *Pastinaca sativa* L., Vienna district, Austria, leg. F. Hendel. 1♂ from larva 28.v.66 on *Heracleum sphondylium* L., Dessau (- Mosigkau), Germany, emerged 26.vi.66, leg. K. H. Zoerner. 1♂ from larva 17.iii.53 on *Heracleum sphondylium* L., Sintra, Portugal, emerged 22.iv.53, leg. K. A. Spencer. 1♂ from larva 29.vii.53 on *Heracleum sphondylium* L., Woodside Park, Middlesex, England, emerged 18.viii.53, leg. G. C. D. Griffiths. 1♂ from larva 31.vii.54 on *Heracleum sphondylium* L., Chilworth, Surrey, England, emerged 18.viii.54, leg. G. C. D. Griffiths. 4♂♂ 4♀♀ from larvae 6.ix.66 on *Heracleum sphondylium* L., Killarney, Ireland, emerged 26.ix-3.x.66 and 6-10.iii.67, leg. G. C. D. Griffiths.

1♂ from larva on *Angelica atropurpurea* L., Ithaca, New York, leg. A. S. Mills (paratype of *angelicella*). 4♂♂ 13♀♀ from larvae 19-27.vi.71 on *Heracleum lanatum* Michx., Elk Island National Park, Alberta, emerged 11-18.vii.71, leg. G. C. D. Griffiths.

*Other records*. — Other Alberta records of this species (as "*spondylii*") are given by Spencer (1969) and Sehgal (1971). These refer to localities in the Edmonton area and George Lake (near Busby). Von Tschirnhaus (in correspondence) has supplied the following record after study of my description and figures: 1♂ from larva 3.vii.71 on *Heracleum sphondylium* L., Neuhoof, N of Lübeck, Schleswig-Holstein, Germany, emerged 21.viii.71. All European records except those stated here must be regarded as doubtful because of possible confusion with *spondylii* (see above under that species).

*Phytomyza sphondyliivora* Spencer 1957

*Phytomyza* sp. Hering, 1956: 280.

*Phytomyza sphondyliivora* Spencer. Spencer, 1957: 23. Holotype ♀, Wiltshire (England), in K. A. Spencer's collection.

*Adult*. — As described for *spondylii*, except as follows.

Orbits more distinctly projecting above eye in lateral view. Posterior ors half to almost as long as anterior ors; two or three pairs of ori. Costal ratio  $mg_2/mg_4$  2.7-3.4. Wing length 2.4 - 2.7 mm.

Thorax colour as in darkest specimens of *spondylii*; mesonotum entirely dark, with sutural triangle scarcely paler (at most dark brown); mesopleuron with only narrow dorsal strip of whitish coloration.

Aedeagus as Fig. 11, 12; basal section with dense strip of dorsal spinules towards right side; medial lobe with pair of long sclerites (not forming loop), without additional small sclerites; distal section without ventral notch, unpigmented except for small mesophallus (strongly pigmented in Dorset specimen, but only weakly so in other specimens). Ejaculatory apodeme as Fig. 13.

*Puparium and third instar larva*. — Described and figured by Hering (1956: 280) (as *Phytomyza* sp.). Mandibles with two alternating teeth; right mandible longer than left. Anterior spiracles two-horned, with 10-12 bulbs; posterior spiracles on short broad processes, with 18 - 22 bulbs in narrow ellipse. Puparia dark brown to black, 2.2-2.4 mm long, strongly arched, with intersegmental boundaries distinctly impressed; anal lobes weakly prominent.

*Mine*. — Larvae leaf-miners on *Heracleum*. Mine (Spencer, 1957, Fig. 3) interparenchymal, pale green when fresh, later turning yellowish; channel broadly linear, in most cases with irregular blotchy areas; faeces deposited as discrete, sparsely scattered particles (Hering, 1957: 525); larvae leaving leaf through semicircular slit before puparium formation.

*Material examined*. — 1♂ paratype from larva 6.vi.54 on *Heracleum sphondylium* L., Corsham, Wilts., England, emerged 11.iv.55, leg. K. A. Spencer. 1♂ from larva 7.vi.63 on *Heracleum sphondylium* L., Portland, Dorset, England, emerged 18.iii.64, leg. K. A. Spencer. 1♂ 1♀ from larvae 20.vi.54 on *Heracleum sphondylium* L., Betchworth, Surrey, England, emerged 17.v and 21.vi.55, leg. G. C. D. Griffiths. Preparations of three larvae, 14.v.61, on *Heracleum sphondylium* L., Cambridge, England, leg. G. C. D. Griffiths.

*Remarks*. — Additional English localities are Hampstead, London (30.v.53 and 3.vii.58) and Luccombe, Isle of Wight (4.vii.64) (sheets in Hering's mine herbarium). I have seen no material of this species from outside southern England. However Hering has referred to it the following herbarium sheets for Austria and Germany (all of *Heracleum sphondylium* L.): Linz (Donau, Austria), 6.vii.29; Straubing (Bavaria, Germany), 11.vi.66; Berlin Botanical Gardens, 15.vi.60; and Jägersburger Wald, near Lorsch (Hessen, Germany), 11.vi.52.

This species is the only *Phytomyza* miner of *Heracleum* which is univoltine in southern England. Its characteristic interparenchymal mines can be confused only with those of the new species next to be described.

*Phytomyza tlingitica* new species

*Adult*. — As described for *spondylii*, except as follows.

Orbital setae very variable between individuals; posterior ors ranging from almost as long as anterior ors to absent (absent in many cases); anterior ori ranging from absent to fully as long as posterior ori (with small third ori on one side in one male). 2-7 peristomal setulae.

Costal ratio  $mg_2/mg_4$  3.9-4.9. Wing length: ♂, 2.5-3.1 mm (mean 2.8 mm); ♀, 2.7-3.4 mm (mean 3.2 mm).

Face paler, largely yellow or yellow-brown, strongly infuscated only along central keel or immediately below antennal bases. Sides of mesonotum contrastingly pale, with sutural triangle entirely whitish or whitish yellow and humeral callus partly so (infuscated only at centre); mesopleuron with broad whitish or whitish yellow dorsal yellow area (about 1/4 of height of mesopleuron); pteropleuron also partly whitish or whitish yellow.

Aedeagus as Fig. 8, 9; basal section without spinules; medial lobe with pair of sclerites, of which the left is longer and more or less confluent at its base with small horizontally orientated sclerite; distal section without ventral notch, unpigmented except for small mesophallus. Ejaculatory apodeme slender (Fig. 10).

*Puparium and third instar larva.* — Mandibles with two more or less alternating teeth; right mandible slightly longer than left. Anterior spiracles with two short horns, with about 10 bulbs in open ellipse; posterior spiracles on short conical processes, with 17-27 bulbs in irregular narrow ellipse. Puparia dark brown or black, 2.3-2.6 mm long, strongly arched, with intersegmental boundaries distinctly impressed; anal lobes not prominent.

*Mine.* — Larvae leaf-miners on *Heracleum*. Mine (Fig. 40B) interparenchymal, pale green when fresh (scarcely contrasting with rest of leaf in reflected light), later indicated by areas of red-brown discoloration; channel basically linear, but broad and strongly convolute, in most cases forming irregular secondary blotch; faeces deposited as fine particles irregularly throughout mine, mostly separated by less than 1 mm; larvae leaving leaf through semicircular slit on lower surface before puparium formation.

*Types.* — Holotype ♂, 10♂♂ 9♀♀ paratypes from larvae 29.vi-7.vii.68 on *Heracleum lanatum* Michx., Chilkat peninsula (near Haines), Alaska, emerged 5.xi-27.xii.68 (forced) and 10-20.v.69, leg. G. C. D. Griffiths.

*Remarks.* — The species-name *tingitica* is based on the name of the Tlingit tribe, which inhabits the Alaska Panhandle.

A remarkable feature of the type series is the frequency of abnormal wing development. Seven of the twenty specimens have one or more complete cross-veins between  $r_{2+3}$  and  $r_{4+5}$ , and others have partial cross-veins or stubs on one of these veins; in addition some specimens have a truncate wing tip. Both types of anomaly are shown by the wing figured (Fig. 36). Only seven specimens (35%) lack all such deviations from the normal *Phytomyza* wing-type. Specimens with venational abnormalities have been reported for many other species of Agromyzidae (see Hering, 1934 and Nowakowski, 1958), but are very rare. The high frequency of their occurrence in *tingitica* is unprecedented, and must surely indicate that the genes concerned have beneficial effects which offset the disadvantage of reduced flight efficiency. The type series was obtained from two samples of leaves collected at points 5 miles apart (Portage Cove and Paradise Cove); the same anomalies are shown in flies from both samples.

#### *Phytomyza angelicastr* Hering 1932

*Phytomyza angelicastr* Hering. Hering, 1932: 576. Hendel, 1934:346. De Meijere, 1938: 88. Syntypes ♂♀, Crossen an Oder (Poland), in Zoologisches Museum, Humboldt Universität, Berlin.

*Adult.* — As described for *spondylii*, except as follows.

Genae in middle 1/4 to 1/3 of eye height. Posterior ors normally about 2/3 as long as anterior ors (but fully as long in some specimens, absent on one side in one male); anterior ori 1/3 to 2/3 as long as posterior ori; orbital setulae one-rowed. 3-4 upcurved peristomal setulae.



Acr in 4-5 irregular rows. Costal ratio  $mg_2/mg_4$  3.0-3.8. Wing length 2.2-2.4 mm.

Centre of frons largely greyish white to ochreous yellow (infuscated anteriorly in paratype); orbits ochreous to brownish; genae yellow or ochreous yellow. Pale dorsal band on mesopleuron very narrow in all specimens.

Aedeagus as Fig. 14, 15; basal section with pair of serrate dorsal strips of sclerotization (about equally developed on both sides) above basal sclerites; main sclerites of medial lobe fused distally, forming point; additional sclerite (not spiniform) at left basal corner of medial lobe, but no similar sclerite on right side; distal section without ventral notch, partly unpigmented, but with conspicuous black mesophallus at base and paired narrow bands of distal pigmentation (distiphallus). Ejaculatory apodeme as Fig. 16.

*Puparium and third instar larva.* — Similar to those of *spondylii*, but with, on average, more numerous spiracular bulbs. Anterior spiracles with 12-18 bulbs; posterior spiracles with 22-28 bulbs (Fig. 37). See also the description of de Meijere (1938:88).

*Mine.* — Larvae leaf-miners on *Angelica*. Mine (Fig. 41) basically linear, but normally convolute (in some cases forming irregular secondary blotch), conspicuous (appearing white in reflected light), formed mainly on upper surface of leaf but with short initial linear channel on lower surface; faeces deposited as fine particles, mostly separated by less than 1 mm; larvae leaving leaf through semicircular slit (on upper or lower surface) before puparium formation.

*Material examined.* — 1♂ paratype from larva 24.viii.32 on *Angelica sylvestris* L., Krosno (Crossen an Oder), Poland, emerged 12.ix.32, leg. M. Hering (no. 4030). 1♂ from larva on *Angelica* sp., München (-Freimann), Germany, emerged 25.i.53, leg. F. Groschke. 1♂ from larva vii.53 on *Angelica sylvestris* L., Grantown, Inverness, Scotland, emerged 26.viii.53, leg. K. A. Spencer. 2♀♀ from larvae 10-17.ix.53 on *Angelica sylvestris* L., Rickmansworth, Herts., England, emerged 5-11.x.53, leg. G. C. D. Griffiths. Preparation of larva, 21.vi.61, on *Angelica sylvestris* L., Woodwalton Fen, Hunts., England, leg. G. C. D. Griffiths.

*Other records.* — The known distribution of this species is summarized as follows. Except where otherwise stated, all records refer to specimens bred from, or mines found on, *Angelica sylvestris* L.

Britain — Widespread and common from South-East England to Inverness (Scotland) and the West coast of Ireland; locality records given by Spencer (1955), Allen (1956), Manning (1956) and Griffiths (1963, 1966, 1968). There are probably three generations a year in southern England (see Allen, 1956 and Griffiths, 1963).

France — Calvados, Normandy (sheet in Hering's mine herbarium).

Belgium — Rixensart (Collart, 1942).

Germany — Probably widespread; in addition to the above record for München, collected by Zoerner (1969) in the Middle Elbe region and by H. Buhr at Mühlhausen, Thuringia (Griffiths, 1966: 873); also sheets in Hering's mine herbarium for Saxony (Görlitz, Lausitz, Bad Elster), Rheinland (Rhöndorf), Mecklenburg (Ribnitz) and Berlin. Von Tschirnhaus (in correspondence) has caught this species near Kiel (Schleswig-Holstein) (6♂♂ 5♀♀, Dobersdorfer See, 2.vi.68; 1♂, Ihlkate, 22.vi.69).

Austria — Sheets in Hering's mine herbarium for Linz (Donau) and Güssen bei St. Georgen.

Poland — Widespread; records additional to the type locality given by Kubska (1961), Beiger (1965a, 1965b, 1970), Griffiths (1966: 873) and Michalska (1970).

Bulgaria — West Rila mountains (Buhr, 1941b).

Denmark — Lolland (Rydén, Lyneborg & Nielsen, 1963).

Norway — Collected at Voss by Grönlien (Hering, 1932).

Sweden — Widespread in the South; records given by Rydén (1937) and Griffiths (1966: 873).

Finland — Recorded by Frey (1946), but the records seem based on caught flies and require checking.

*Phytomyza lanati* Spencer 1966

*Phytomyza lanati* Spencer. Spencer, 1966: 108.—1969: 250. Holotype ♂, Berkeley Hills (California), in U. S. National Museum, Washington.

I have not seen material of this species, of which only two specimens are known. Spencer's descriptions suggest that it is not separable from *spondylii* on external characters. His figures of the aedeagus (♂) indicate the following differences from *spondylii*:— basal section without spinules; pair of additional serrate strips of sclerotization below main sclerites of medial lobe; distal section without ventral notch, partly unpigmented but with small pigmented mesophallus (more widely separated from basal section than in other species of *spondylii* subgroup) and paired narrow bands of distal pigmentation (distiphallus).

This species was originally described (Spencer, 1966) from a mixed sample containing also specimens of *spondylii heracleiphaga*. Some of the paratypes were later found to belong to the latter taxon. Only the holotype male (bred by M. J. & C. A. Tauber from *Heracleum lanatum* Michx. at Strawberry Canyon, Berkeley Hills, California, emerged 7.vi.64) and a specimen caught at Jasper, Alberta (19.vi.66) are correctly referred to this species (Spencer, 1969).

The holotype is believed to have been bred from linear upper-surface mines similar to those of *spondylii*. Owing to the previous confusion between this species and *spondylii heracleiphaga*, it is not clear whether the life-history information published by Tauber & Tauber (1966, 1968) in fact refers to this species. Their work needs to be supplemented by further studies to clarify the identity of the species concerned.

*Phytomyza archangelicae* Hering 1937

*Phytomyza archangelicae* Hering. Hering, 1937: 566. De Meijere, 1937: 212. Griffiths, 1964: 400. Syntypes ♂♀, Mecklenburg (Germany), in Zoologisches Museum, Humboldt Universität, Berlin.

*Phytomyza nilssoni* Rydén. Hering, 1956: 275. Rydén, 1956: 199. Holotype ♂, Abisko (Sweden), in Zoological Institute, University of Lund. Synonymy after Griffiths, 1964: 400.

*Adult.* — Head with orbits not or only narrowly projecting above eye in lateral view; genae in middle 1/4 to 1/3 of eye height; eyes with only sparse fine pubescence. Frons at level of front ocellus about twice width of eye. Ors directed posteriorly, ori directed inwardly; posterior ors half to almost as long as anterior ors (about half in most specimens); anterior ori 1/2 to 3/4 as long as posterior ori in most specimens, but weak or absent in a few; orbital setulae few (1-4), in one row. Peristomal margin with vibrissa and 4-5 upcurved peristomal setulae. Third antennal article rounded distally, with short pubescence.

2 + 1 or 3 + 1 dc (see note in Griffiths, 1964); acr in four irregular rows; 6-10 presutural ia; 3-8 postsutural ia; inner pa about half as long as outer pa.

Second cross-vein (m-m) absent. Costal ratio  $mg_2/mg_4$  3.0-3.7. Wing length 2.3-2.7 mm.

Colour almost entirely dark. Centre of frons dark brown; genae brown or yellow-brown. Labella yellow. Thorax grey-dusted over black ground colour, only weakly shining, with pale coloration only along notopleural and mesopleural sutures and at posterior corner of humeral callus. Wing base and squamae yellowish white, latter with dark fringe. Legs largely dark with tips of front femora contrastingly yellow; tips of other femora less contrasting, yellow-brown to virtually black. Basal cone of ovipositor (♀) grey dusted on dorsal surface on about basal third.

Male postabdomen with 8th sternum fused with 6th tergum. Telomeres partly delimited from periandrium by suture on outer side, bearing dense group of setulae. Pregonites large, weakly pigmented, extending ventrally (shielding base of aedeagus at rest). Aedeagal hood with two pairs of lateral sclerites (the more dorsal pair rather ill-defined). Aedeagus as Fig. 17, 18; basal sclerites very long, with left basal sclerite appearing sinuate in lateral view; three spinules on left side near apex of basal section; medial lobe scarcely differentiated, but its right sclerite retained (small slender sclerite near apex of right basal sclerite); distal section very short, with small unpaired sclerite (mesophallus) near base. Ejaculatory apodeme small (Fig. 19).

*Puparium and third instar larva.* — Described in detail by de Meijere (1937: 212) and Hering (1956: 275) (as *nilssoni*). Mandibles slender, with two more or less alternating teeth; right mandible slightly longer than left. Ventral process of paraclypeal phragma short. Anterior spiracles two-horned, with 8-14 bulbs in widely open ellipse; posterior spiracles on short broad processes, with 20-28 bulbs in narrow open ellipse (Fig. 39). Puparia dark brown to black, 1.6-2.0 mm long, strongly arched, with intersegmental boundaries distinctly impressed; anal lobes not prominent.

*Mine.* — Larvae leaf-miners on *Angelica*. Mine (Fig. 42) entirely linear, 7-10 cm long, about 2 mm wide terminally; faeces deposited as fine particles or in beaded strips on alternate sides of mine channel; mine conspicuous, appearing white in reflected light, formed mainly on upper surface of leaf but with short initial channel on lower surface; larvae leaving leaf through semicircular slit (on upper or lower surface) before puparium formation.

A figure of the leaf mine has previously been published by Rydén (1956).

*Material examined.* — 1 ♂ paratype from larvae 17.vi.36 on *Angelica archangelica* L., Neuhaus, Mecklenburg, Germany, emerged 6.vii.36, leg. H. Buhr. 3 ♂♂ 4 ♀♀, Kirkjubøur and Kirkjubøurhólmur, Streymoy, Faroe Islands, 3.vi.26 (caught), leg. P. J. Kryger. 4 ♂♂ from larvae vii.54 on *Angelica archangelica* L., Abisko and Kopparäsen, Torne Lappmark, Sweden, emerged 4-11.viii.54, leg. N. Rydén (holotype and paratypes of *nilssoni*).

4 ♂♂ 4 ♀♀ from larvae 26-30.vi.68 on *Angelica genuflexa* Nutt., Chilkat peninsula (near Haines), Alaska, emerged 24-28.vii.68 and 8.x.68 (1 ♀), leg. G. C. D. Griffiths; also parasitized larvae, same dates and locality, on *Angelica lucida* L. Empty mines on *Angelica genuflexa* Nutt. at Starrigavan, Sitka, Alaska (24.viii.69).

*Remarks.* — For discussion of synonymy and types, see my previous paper (Griffiths, 1964).

In addition to localities listed above, this species is reported on *Angelica archangelica* L. in North-West Poland; common in the Stettin district (Hering, 1937), Isle of Wolin and Dziwnów Peninsula (Nowakowski, 1954), and at Międzyzdroje and Drawsk-on-Notec (Beiger, 1958). There is also a sheet of the same plant from southern Sweden (Råå near Hälsinborg, 14.viii.50) in Hering's mine herbarium. The discovery of this species in Alaska suggests that it is widely distributed at high latitudes. Whether it occurs in the mountains of Central Europe requires confirmation. Buhr (1964) has recorded it on *Angelica sylvestris* L. in the mountains of Saxony, presumably on the basis of mines similar to those recorded from South Moravia (Czechoslovakia) by Hering (1935) as *Phytomyza* spec. (no. 201). The figure

of mines attributed to *archangelicae* by Hering (1957) is based on this Moravian material (the same figure as on page 60 of his 1935 work). I have traced no flies bred from these collections in Moravia and Saxony, and regard the identity of the species concerned as unconfirmed.

*Phytomyza arnaudi* Sasakawa 1955

*Phytomyza arnaudi* Sasakawa. Sasakawa, 1955: 93.—1961a:441. Holotype ♂, Kyoto (Japan), in Entomological Laboratory, Saikyo University.

Described by Sasakawa (1955) on the basis of 10♂♂ 13♀♀ bred from *Angelica miqueliana* Maxim. at Kibune, Kyoto. In his 1961 work he also lists *Osmorhiza aristata* Makino & Yabe as a host, but gives no details of this record. Unless based on dissection of bred males, this record should be regarded as doubtful. In North America *Osmorhiza* and *Angelica* do not have any *Phytomyza* miners in common where they grow together.

I have seen no material of this species. The form of its aedeagus (Sasakawa, 1961a, Fig. 112d) suggests that it is very close to *archangelicae*. I base this opinion particularly on the presence of spinules in similar position near the apex of the basal section and the similarity of the very short distal section in both species.

*Phytomyza polycladae* Sasakawa 1955

*Phytomyza polycladae* Sasakawa. Sasakawa, 1955:95.—1961a:465. Holotype ♀, Hokkaido (Japan), in Entomological Laboratory, Saikyo University.

Described by Sasakawa (1955) on the basis of a female bred from *Angelica polyclada* Franch. at Sapporo, Hokkaido. In his 1961 work he records additional material bred from *Sanicula elate* Ham. var. *chinensis* Makino. Unfortunately it is not stated whether the new figures in this work (including those of the male genitalia) are based on material from *Angelica* or *Sanicula*. These plant genera have no *Phytomyza* miners in common in Europe and North America. Unless the genitalia of males bred from both hosts have been compared, the reference of the material from *Sanicula* to *polycladae* is suspect. If no male from *Angelica* was available, we cannot be sure that Sasakawa's (1961a) figures of the male genitalia refer to the true *polycladae*. I have seen no material referred to this species.

(b) the *Phytomyza angelicae* group

The species referred to this group all show a uniform type of aedeagus in which the distal section contains a pair of slender tubules arising from a cylindrical basal area of sclerotization; the spine-like processes (spinules) characteristic of most species of the *albiceps* group are lacking. The species of this group treated in this paper are *P. angelicae* Kaltenbach, *P. kibunensis* Sasakawa, *P. latifolii* Groschke, *P. heracleana* Hering and *P. angelicivora* Hering. Other species known to belong to this group are *P. pauliloewi* Hendel (Nowakowski, 1962), *P. selini* Hering (Nowakowski, 1962), *P. silai* Hering and *P. aconiti* Hendel. The reference of the last species (feeding on the ranunculaceous *Aconitum* and *Delphinium*) to this group may seem surprising, since all the other species feed on Umbelliferae. But the similarity between *aconiti* and the other species in the form of the aedeagus (Spencer, 1969, Fig. 390, 391) is clear enough, and the possibility of this relationship was already suggested by my report that the parasitoid *Dacnusa fuscipes* Griffiths (Hymenoptera, Braconidae) develops both on *aconiti* and *angelicae* (Griffiths, 1966:818).

Nowakowski (1962:105) has included the *angelicae* group as a subgroup of the *albiceps*

group, but gives no characterization in support of this classification. I prefer to separate the *angelicae* group from the *albiceps* group, since it is possible that the former is more closely related to some of the groups of Ranunculaceae-feeders. Further studies on the latter are needed to clarify this point.

I have previously drawn attention (Griffiths, 1972b) to the high variability in the length of the posterior ors in the *albiceps* group. In the species of the *angelicae* group treated in this paper, the length of this bristle is less variable. I think that a valid distinction can be drawn between species with strong posterior ors (*angelicae*, *pauliloewi*, *latifolii* and *aconiti*) and those in which this is less than half as long as the anterior ors (*heracleana*, *kibunensis*, *angelicivora*, *silai* and *selini*).

*Phytomyza angelicae* Kaltenbach 1874

*Phytomyza angelicae* Kaltenbach. Kaltenbach, 1874:279. Brischke, 1880:255. Hendel, 1920:159.—1934:344. De Meijere, 1926:243. Hering, 1927:115. Allen, 1956:125.—1957:172. Griffiths, 1964:400. Types lost; type-locality Germany.

*Phytomyza laserpitii* Hendel. Hendel, 1924:140.—1935:424. De Meijere, 1926:270.—1938:91. Hering, 1927:115. Syntypes ♂♀, Walchsee (Austria), in Naturhistorisches Museum, Vienna. New synonymy.

*Adult*.—Head with orbits not or only very narrowly projecting above eye in lateral view; genae in middle 1/4 to 1/3 of eye height; eyes with only sparse fine pubescence. Frons at level of front ocellus 2-2½ times width of eye. At least four well-developed pairs of orbital setae (two ors and two ori) present; posterior ors posteriorly directed, half to fully as long as anterior ors, anterior ors directed posteriorly or inwardly (normally only two pairs of ors present, but third ors present on one side in a few specimens); two pairs of long, inwardly directed ori present and in some specimens also shorter third pair; orbital setulae one-rowed. Peristomal margin with vibrissa and 3-6 upcurved peristomal setulae. Third antennal article rounded distally, with short pubescence. Palpi large, somewhat expanded.

3 + 1 dc; acr in 4 irregular rows; presutural ia numerous; 2-9 postsutural ia; inner pa 1/2 to 2/3 as long as outer pa.

Second cross-vein (m-m) absent. Costal ratio  $mg_2/mg_4$  2.5-3.5 (mean 2.95). Wing length 2.0-3.1 mm (means: ♂, 2.55 mm; ♀, 2.8 mm).

Frons and orbits yellow, except dark vertex and ocellar plate (vte on dark ground, vti on boundary between dark and yellow ground). Face yellow at sides, with variable degree of infuscation in antennal pits. Genae yellow. Occiput dark. Antennae entirely dark, at most with first article and outer side of second article brown. Palpi black; labella yellow. Mesonotum densely grey-dusted, not shining, almost entirely dark, at most with traces of brown or yellow coloration on upper part of sutural triangle, at corners of humeral callus and on postalar callus; scutellum dark; mesopleuron largely dark, with only narrow dorsal strip of pale coloration; other pleura dark, but with some pale coloration along sutures (especially mesopleural suture). Wing base and squamae yellowish white, latter with dark fringe. Legs dark, with tips of femora yellow (in some specimens only those of front femora distinctly contrasting). Abdomen largely dark brown, in some specimens with narrowly yellow hind margins of terga. Basal cone of ovipositor (♀) largely shining, grey dusted only narrowly at base on dorsal surface.

Male postabdomen with 8th sternum fused with 6th tergum. Telomeres not delimited from perianthrium, bearing only fine setulae. Pregonites large, distinctly pigmented, extending ventrally (shielding base of aedeagus at rest). Aedeagal hood with two pairs of lateral sclerites. Aedeagus as Fig. 20, 21; right basal sclerite expanded at base; left basal sclerite varia-

ble in width (compare Fig. 21 and my figure of an Icelandic specimen (Griffiths, 1964, Fig. 2)); medial lobe with pair of well-defined sclerites; distal section with pair of slender tubules arising from cylindrical basal area of sclerotization. Ejaculatory bulb and apodeme as Fig. 22, with sides of bulb distinctly pigmented.

*Puparium and third instar larva.*— Described by de Meijere (1926:243, 270 and 1938: 91) and Allen (1957). Mandibles with two alternating teeth; right mandible longer than left. Anterior spiracles with 10-13 bulbs in widely open ellipse; posterior spiracles (Fig. 38) on short conical processes, with 15-22 bulbs in broad ellipse (nearly circular). Puparia brown or black, 1.9-2.5 mm long, strongly arched, with intersegmental boundaries distinctly impressed; anal lobes prominent.

*Mine.*— Larvae leaf-miners on *Angelica*, *Heracleum* and *Laserpitium*. Mine (Fig. 43) primary blotch (without initial linear channel) on upper surface of leaf, with faeces irregularly deposited as particles throughout mine; mine appearing largely whitish or light green in reflected light, but with area consumed by first-instar larvae yellow or brownish; most mines communal, formed by more than one larva; larvae leaving leaf through semicircular slits (on upper or lower surface) before puparium formation.

The yellowish or brownish area produced by first-instar larvae is not always in the centre of the mine, as implied in Hering's (1957) key to miners of *Angelica*. A figure of mines of this species on *Angelica* is included in that work. Beiger (1960) gives a figure of a mine on *Laserpitium*. Spencer's (1969:286) figure of a mine on *Heracleum* from George Lake (Alberta) also refers to this species.

*Material examined.* — 8♂♂ 10♀♀ from larvae 9.viii.53 on *Angelica sylvestris* L., Pangbourne, Berks., England, emerged 26-30.viii.53, leg. G. C. D. Griffiths. 2♀♀ from larvae 15.viii.53 on *Angelica sylvestris* L., Bookham, Surrey, England, emerged 7.ix.53, leg. G. C. D. Griffiths. 1♂ 1♀ from larvae 8.xi.53 on *Angelica sylvestris* L., Brookman's Park, Herts., England, emerged 11.v and 2.vi.54, leg. G. C. D. Griffiths; 2♂♂ 1♀ from larvae 17.vi.62, same plant and locality, emerged 10-11.vii.62, leg. G. C. D. Griffiths.

4 ex. from larvae 30.vii.62 on *Angelica sylvestris* L., Skaftafell, Iceland, emerged 18.ii-9.iii.63, leg. H. Andersson (Griffiths, 1964).

1♂ 1♀ from larvae on *Laserpitium latifolium* L., Walchsee, Tirol, Austria, emerged 15.viii.23 and 18.iii.24, leg. F. Hendel (syntypes of *laserpitii*). 1♂ from larva 25.vii.55 on *Laserpitium latifolium* L., Névache, Hautes Alpes, France, emerged 26.v.56, leg. K. A. Spencer. 1♂ from larva on *Laserpitium latifolium* L., Vals, Switzerland, emerged 7.iii.30, leg. W. Hopp. 1♂ from larva on *Laserpitium latifolium* L., Schwäbische Jura, Germany, emerged 2.iv.23, leg. M. Hering (no. 2254) (paratype of *laserpitii*). 1♂ from larva on *Angelica sylvestris* L., Bredow bei Nauen, Germany, emerged 8.vii.23, leg. M. Hering (no. 2221). 1♂ from larva 3.vii.29 on *Angelica sylvestris* L., Berlin (Rüdersdorf), Germany, emerged 21.ix.29, leg. M. Hering. 1♂ from larva 14.v.66 on *Angelica sylvestris* L., Möst (near Dessau), Germany, emerged 25.vi.66, leg. K. H. Zoerner. 6♂♂ 4♀♀ from larvae 18.viii.65 on *Angelica sylvestris* L., Mühlhausen (Stadtwald), Thuringia, Germany, emerged 6-10.ix.65, leg. H. Buhr (no. 2609); 6♂♂ 7♀♀ from larvae 4.x.65, same plant and locality, emerged 22-23.x.65, leg. H. Buhr (nos. 2691 & 2692); 19♂♂ from larvae 7.viii.67, same plant and locality, emerged 24-31.viii.67, leg. H. Buhr (no. 3561). 1♂ 1♀ from larvae 4.viii.24 on *Angelica archangelica* L., Stettin, Poland, emerged 28.viii.24, leg. Enderlein.

9♂♂ 9♀♀ from larvae 26-30.vi.68 on *Heracleum lanatum* Michx., Chilkat peninsula (near Haines), Alaska, emerged 5-28.v.69, leg. G. C. D. Griffiths; 1♂ from larvae on *Angelica gen- uflexa* Nutt., same dates and locality, emerged 10.v.69, leg. G. C. D. Griffiths; 14♂♂ 26♀♀ from larvae on *Angelica lucida* L., same dates and locality, emerged 8.v-22.vi.69, leg. G. C. D.

Griffiths. 47♂♂ 30♀♀ from larvae 19-22.vi.71 on *Heracleum lanatum* Michx., Elk Island National Park, Alberta, emerged 10-17.vii.71 (74 ex.) and 10-11.v.72 (2♂♂ 1♀), leg. G. C. D. Griffiths.

*Other records.* — Other records of this species for Europe are summarized as follows. The records listed above are the first for North America.

Britain — Widespread and common on *Angelica sylvestris* L., from South-East England to the West coast of Ireland (northern limit not known); locality records given by Allen (1956), Manning (1956) and Griffiths (1966, 1968).

France — Forges d'Abel, Pyrenees (1200 metres), on *Angelica razulii* Gouan (sheet in Hering's mine herbarium).

Holland — Collected on *Angelica sylvestris* L. by de Meijere (1926: 243).

Germany — Widespread and common on *Angelica* and *Laserpitium*; locality records given by Voigt (1929), Buhr (1932, 1941a, 1960, 1964), Griffiths (1966: 796, 810, 873) and Zoerner (1969); also numerous sheets in Hering's mine herbarium. Von Tschirnhaus (in correspondence) has taken this species at Döbersdorfer See, near Kiel (Schleswig-Holstein).

Austria — Collections on *Laserpitium* recorded by Hendel (1924) and de Meijere (1938: 91); also sheets for *Angelica sylvestris* L. and *Laserpitium* in Hering's mine herbarium.

Italy — Alto Adige, on *Laserpitium* (Hartig, 1939).

Poland — Widespread, on *Angelica* and *Laserpitium*; locality records given by Brischke (1880), Karl (1936), Nunberg (1947), Nowakowski (1954), Beiger (1960, 1965a, 1965b, 1970), Kubska (1961), Griffiths (1966: 796, 856) and Michalska (1970).

Czechoslovakia — On *Angelica sylvestris* L. (Starý, 1930).

Denmark — Collected on *Angelica* by Sønnerup (1949).

Sweden — Widespread, on *Angelica* and *Laserpitium*; locality records given by Rydén (1937, 1940, 1951, 1952) and Lundqvist (1949).

Finland — Photograph of mines on *Angelica sylvestris* L. in Linnaniemi (1913, Tafel VII); recorded on *Angelica* and *Laserpitium* by Frey (1937, 1946).

Russia — Livny and Moscow regions, on *Angelica sylvestris* L. (Braschnikow, 1897; Rohden-dorf, 1960).

*Remarks.* — Hendel (1935:424) has already cast doubt on his previous separation of *laserpitii* as a distinct species. I can find no difference between flies bred from *Angelica* and *Laserpitium*, and therefore formally synonymize *laserpitii* with *angelicae*.

The taxon from Japan described by Sasakawa (1953, 1961a) as *Phytomyza angelicae kibunensis* is in my opinion a distinct species (see below). The Japanese vicariant of *angelicae* is more probably represented by specimens bred by M. Kuroda from communal blotch-mines on *Angelica decursiva* Franch. & Savat. (1♂ 2♀♀, Tottori prefecture, vi.67, now in K.A. Spencer's collection). These agree with the above description of *angelicae*, except as follows:—genae narrower, 1/6-1/4 of eye height; palpi more strongly enlarged; frons and genae orange-yellow; distal section of aedeagus (♂) with shorter distal tubules (Fig. 23). It is possible that these specimens are referable to the taxon described by Sasakawa (1961a: 443) as *Phytomyza bifida*, on the basis of caught specimens from Hokkaido. However the sclerites of the medial lobe in the bred male are not fused with the basal sclerites as indicated in the description of *bifida*. Until more material has been obtained, I must leave open the questions of whether Kuroda's specimens represent a distinct species or a race of *angelicae*, and of whether Sasakawa's name *bifida* refers to the same taxon.

*Phytomyza kibunensis* Sasakawa 1953, new status

*Phytomyza angelicae kibunensis* Sasakawa. Sasakawa, 1953: 13.—1961a:440. Holotype ♂, Kyoto (Japan), in Entomological Laboratory, Saikyo University.

See the detailed descriptions of Sasakawa (1953, 1961a). I have noted the following differences from *angelicae*:— posterior ors short or absent, only two ori present (anterior ori shorter than posterior ori); palpi smaller; costal ratio  $mg_2/mg_4$  higher, 3.5-3.9; aedeagus (♂) (Fig. 24, 25) with distal tubules and sclerites of medial lobe shorter. The puparium and third instar larvae have a similar range of spiracular bulb numbers to that of *angelicae* (anterior spiracles with about 10 bulbs; posterior spiracles with 17-20 bulbs) (Sasakawa, 1953). Mine (Sasakawa, 1961a, Fig. 1109) primarily linear, formed by single larva, with irregular blotchy areas terminally; faeces deposited as fine particles, arranged in strips on alternate sides of linear parts of mine; larvae leaving leaf through semicircular slit (on upper or lower surface) before puparium formation.

*Material examined.* — 1♂ paratype from larva v.51 on *Angelica polyclada* Franch., Kibune, Kyoto, Japan, emerged 5.vi.51, leg. M. Sasakawa.

*Remarks.*— The type series (2♂♂ 5♀♀) was bred from *Angelica polyclada* Franch. and *A. kiusiana* Maxim. at Kibune (Sasakawa, 1953). Subsequently Sasakawa (1961b) has listed *Heracleum lanatum* Michx. as a host, but I do not know whether this record has been authenticated by study of bred flies.

While *kibunensis* clearly belongs to the *angelicae*-group, I do not accept Sasakawa's interpretation that it is a subspecies of *angelicae*. The true *angelicae* is characterized by large palpi and at least four strong orbital setae, while in *kibunensis* the posterior ors and anterior ori are weak and the palpi smaller. In these respects *kibunensis* more closely resembles *heracleana* than *angelicae*. The mines of *kibunensis* are also very different from those of *angelicae*. Since flies more closely resembling *angelicae* have recently been obtained in Japan from communal blotch-mines similar to those of *angelicae* (see above under that species), I think it must be concluded that *kibunensis* is not the Japanese vicariant of *angelicae*. Full specific rank is therefore accorded.

*Phytomyza latifolii* Groschke 1957

*Phytomyza spec.* Hering, 1936: 299 (no. 1467). Hartig, 1939:454.

*Phytomyza latifolii* Groschke. Groschke and Hering, 1957: 128. Hering, 1957: 597. Holotype ♂, Bavaria (Germany), in Staatliches Museum für Naturkunde, Ludwigsburg.

*Adult.* — External form of holotype as described by Groschke (Groschke and Hering, 1957), differing clearly from *angelicae* as follows: only one ori present; palpi relatively smaller; head darker, with frons and genae deep golden yellow and face largely infuscated. Wing length 2.2 mm (not 1.2 as stated in the original description).

Male postabdomen as described for *angelicae*, except as follows. Telomeres partly delimited from perianthrium by suture on outer side. Aedeagus (Fig. 27, 28) with sclerites of medial lobe longer, almost forming loop; terminal tubules of distal section larger, curved upwards so that their apices are posteriorly directed. Ejaculatory apodeme larger (Fig. 29).

*Puparium and third instar larva.* — Puparium of holotype very similar to that of *angelicae*, 2.2 mm long, with prominent anal lobes; anterior spiracles with 10 bulbs; posterior spiracles with 16 bulbs in broad ellipse.

*Mine.* — Larvae leaf-miners on *Laserpitium latifolium* L. Mine (Hering, 1936 and 1957) linear, confined to upper surface of leaf, initially narrow and convolute but strongly widened



to about 2 mm terminally, in many cases branched; faeces deposited as discrete particles in two rows; larvae leaving leaf through semicircular slit on upper surface before puparium formation.

Photographs or figures of the leaf mines have been published by Hartig (1939), Hering (1957) and Beiger (1960).

*Material examined.* — Holotype ♂ from larva 11.viii.51 on *Laserpitium latifolium* L., Kessel am Königssee (near Berchtesgaden), Bavaria, Germany, emerged 28.iv.52, leg. F. Groschke.

*Other records.* — Additional records of this species are as follows.

Austria — Kunatal, Tirol (1500 metres), 27.vii.47, leg. Klimesch (sheet in Hering's mine herbarium); Stanzach im Lechtal (Tirol), 25-26.viii.37, leg. H. Buhr (de Meijere, 1938:95).

Italy — Madonna di Campiglio, Alto Adige (Hartig, 1939).

Poland — Ojców National Park (Góra Koronna), larvae common in June in shrub association (Beiger, 1960).

Spencer's (in Groschke and Hering, 1957) record for France (Névache, Hautes Alpes) is doubtful, as the only adult fly obtained from his sample belongs to *angelicae*.

### *Phytomyza heracleana* Hering 1937

*Phytomyza heracleana* Hering. Hering, 1937:582.—1957:525. De Meijere, 1937: 219. Syn-type ♂, Ribnitz (Germany), in K. A. Spencer's collection.

*Adult.* — Head with orbits not or only very narrowly projecting above eye in lateral view; genae in middle 1/4 to 1/3 of eye height; eyes with only sparse fine pubescence. Frons at level of front ocellus 2-2½ times width of eye. At most four orbital setae (two ors and two ori) present; posterior ors not more than half as long as anterior ors, absent in some specimens; anterior ori 1/2 to 2/3 as long as posterior ori; orbital setulae more or less one-rowed. Peristomal margin with vibrissa and 3-4 upcurved peristomal setulae. Third antennal article rounded distally, with short pubescence. Palpi relatively smaller than in *angelicae*.

3 + 1 dc; acr in 3-4 irregular rows; 3-6 presutural ia; 1-7 postsutural ia; inner pa at most half as long as outer pa (absent in one specimen).

Second cross-vein (m-m) absent. Costal ratio  $mg_2/mg_4$  2.8-3.8. Wing length 1.9-2.3 mm.

Frons and orbits yellow, except dark vertex and ocellar plate (vte on dark ground, vti on boundary between dark and yellow ground). Face largely yellow, only weakly infuscated in antennal pits. Genae yellow. Occiput dark. Antennae with first article yellow-brown, second article brown, third article black. Palpi black; labella yellow. Mesonotum scarcely shining, densely grey dusted over black ground-colour centrally, brownish at sides (especially on sutural triangle), with traces of yellow coloration only at corners of humeral callus; scutellum dark; mesopleuron largely dark, with narrow yellowish-white dorsal strip; other pleura dark, but with some pale coloration along sutures (especially mesopleural suture). Wing base and squamae yellowish white, latter with dark fringe. Legs dark, with tips of front femora contrastingly yellow; tips of other femora less contrasting, dull yellow to brown. Abdomen dark brown. Basal cone of ovipositor (♀) largely shining, without grey-dusting on dorsal surface.

Male postabdomen as described for *angelicae*, except as follows. Telomeres partly delimited from perianthidium by suture on outer side. Aedeagus (Fig. 30, 31) with sclerites of medial lobe longer, broadened ventrally, almost forming loop; distal section with terminal tubules conspicuously angled and curved upwards distally. Ejaculatory apodeme much larger (Fig. 32).

*Puparium and third instar larva.* — Described by de Meijere (1937:219), very similar to those of *angelicae*. Anterior spiracles with about 10 bulbs; posterior spiracles with 14-20 bulbs in broad ellipse. Puparia 1.8-2.0 mm long, with prominent anal lobes.

*Mine.* — Larvae leaf-miners on *Heracleum*. Mine (Hering, 1957:525) (Fig. 44) with short initial linear channel on lower surface; then becoming largely interparenchymal blotch (pale green when fresh) produced by larval feeding on upper layer of spongy parenchyma, with marbled appearance caused by scattered holes eaten in palisade parenchyma; old mines indicated by red-brown or yellowish discoloration; faeces deposited as fine particles throughout mine; larvae leaving leaf through semicircular slit on lower surface before puparium formation.

*Material examined.* — 4♂♂ from larvae on *Heracleum sphondylium* L., Berlin Botanical Gardens, Germany, emerged 22.ii-9.iii.51, leg. E. M. Hering (no. 5690). 1♂ from larva 2l.viii.56 on *Heracleum sphondylium* L., Grasmere, Westmorland, England, emerged 23.v.57, leg. K. A. Spencer.

*Other records.* — The distribution of this species, based on collections of larvae on *Heracleum (sphondylium)* where not otherwise stated), is summarized as follows.

Britain — Localities additional to that stated above given by Spencer (1953) and Griffiths (1966:792); also sheet for Hull in Hering's mine herbarium.

France — Verson near Caen, 30v.42 (sheet in Hering's mine herbarium).

Germany — Additional localities given by Buhr (1941a). Von Tschirnhaus (in correspondence) has supplied the following record: 7♂♂ 8♀♀ from larvae 3.vii.71 on *Heracleum sphondylium* L., Neuhoof, N of Lübeck (Schleswig-Holstein), emerged 23.iii-3.iv.72.

Austria — Tirol (Buhr, 1941a).

Hungary — Collected by Spencer at Janoshegy near Budapest (Griffiths, 1966:792).

Bulgaria — West Rila mountains (Buhr, 1941b).

Poland — Localities given by Buhr (1941a), Nowakowski (1954), Beiger (1960) and Griffiths (1966:835).

Denmark — Bornholm (Buhr, 1941a).

Sweden — Localities given by Lundqvist (1949), Hering (1951) (on *Heracleum mantegazzianum* Sommier & Levier) and Rydén (1952).

Norway — Oslo Botanical Gardens (Rydén, 1955).

*Remarks.* — This species has been reported on various other genera of Umbelliferae additional to *Heracleum*, as follows: *Angelica* (Hering, 1957), *Caucalis* (Hering, 1957), *Laser* (Hering, 1957), *Laserpitium* (Hering, 1957; Beiger, 1960), *Pastinaca* (Buhr, 1941a, 1941b and 1954; Hering, 1957), *Peucedanum* (Hering, 1957; Beiger, 1960), *Pimpinella* (Buhr, 1941a; Hering, 1957; Beiger, 1960 and 1965a) and *Seseli* (including *Libanotis*) (Buhr, 1941a; Hering, 1957; Rohdendorf, 1960; Beiger, 1960 and 1965a). The validity of all these records should be checked, since I have not traced any flies bred from these plants.

There is no evidence of the occurrence of *heracleana* in North America, for the mines on *Heracleum* which Spencer (1969:275) suggested were produced by this species have proved to be produced by *angelicae*.

#### *Phytomyza angelicivora* Hering 1924

*Phytomyza* n.sp.? Braschnikow, 1897:30.

*Phytomyza angelicivora* Hering. Hering, 1924:225.—1927: 126. De Meijere, 1926:244. Hendel, 1934:347. Holotype ♂, Berlin (Germany), in Zoologisches Museum, Humboldt Universität, Berlin.

*Phytomyza* sp. De Meijere, 1938:94.

*Adult.* — Head with orbits only very narrowly projecting above eye in lateral view; genae in middle about 1/3 of eye height; eyes with only sparse fine pubescence. Frons at level of front ocellus about twice width of eye. Only one strong ors (posteriorly directed) present; posterior ors vestigial or absent; anterior ori less than half as long as posterior ori; 2-4 weak orbital setulae in one row. Peristomal margin with vibrissa and 2-4 upcurved peristomal setulae. Third antennal article rounded distally, with short white pubescence. Palpi somewhat expanded.

3 + 1 dc; acr few, in two rows; 2-4 presutural ia; only 1-2 postsutural ia; inner pa about half as long as outer pa.

Second cross-vein (m-m) absent. Costal ratio  $mg_2/mg_4$  2.6-3.0. Wing length 1.5-2.3 mm.

Frons and orbits yellow, except dark ocellar plate; dark colour of vertex extending only to base of vte (vti on yellow ground). Face entirely yellow, without trace of infuscation. Genae yellow. Occiput largely dark, but yellow at sides ventrally. Antennae with first article yellow, second article yellow-brown or reddish, third article dark brown to black. Palpi black; labella yellow. Mesonotum densely grey-dusted, not shining, dark centrally but with broad yellow side bands (humeral callus yellow with brown area in centre; sutural triangle completely yellow); scutellum largely dark, with traces of pale coloration at basal corners; mesopleuron broadly yellow on dorsal half to two-thirds; other pleura dark, but with yellow or whitish coloration along sutures. Wing base and squamae yellowish white (including squamal fringe). Coxae dark; femora largely dark, with contrastingly yellow tips; tibiae and tarsi brown. Abdomen brown, with contrasting narrow yellow band along sides of terga. Basal cone of ovipositor (♀) largely shining, grey dusted only narrowly at base on dorsal surface.

Male postabdomen as described for *angelicae*, except as follows. Aedeagus (Fig. 33, 34) with sclerites of medial lobe relatively longer, almost forming loop; distal section with terminal tubules shorter and cylindrical basal area more closed ventrally. Ejaculatory apodeme as Fig. 35.

*Puparium and third instar larva.* — Described by de Meijere (1926:244, and 1938:94). Mandibles with two alternating teeth; right mandible longer than left. Anterior spiracles with 8-16 bulbs; posterior spiracles with 13-22 bulbs in rounded, partly open ellipse. Puparia dark brown, 1.5-1.6 mm long, strongly arched, with intersegmental boundaries distinctly impressed; anal lobes not prominent.

*Mine.* — Larvae leaf-miners on *Angelica palustris* (Besser). Mine (Hering, 1924 and 1927) with initial linear channel on lower surface, then with broader whitish channel following leaf margin on upper surface (becoming more or less blotchy terminally); faeces irregularly distributed, in places forming beaded strips; larvae leaving leaf through semicircular slit before puparium formation.

*Material examined.* — Holotype ♂, 1♀ paratype from larvae 24.vi.23 on *Angelica palustris* (Besser), Berlin (Brieselang), Germany, emerged 15.vii.23, leg. M. Hering (no. 2285); 1♂, same plant and locality, emerged 26.vi.24, leg M. Hering (no.2454) (incorrectly labelled as type by Hendel, for the emergence date is later than publication of the description); 1♂ from larva 5.vi.29, same plant and locality, emerged 27.vi.29, leg M. Hering (no. 3395).

*Other records.* — This species can be reliably recorded only for Russia (Livny district; Braschnikow, 1897) and East Germany. Published German localities in addition to the type locality are: Güntersberg-an-Oder (Hering, 1924), Nauen (de Meijere, 1938, as *Phytomyza* sp.), Pasewalk (Buhr, 1954) and Bräsenbruch (Zoerner, 1969). De Meijere's (1937:211) record for Holland is probably incorrect, as based on larvae from *Angelica sylvestris* L. with more numerous spiracular bulbs (described as "*Phytomyza obscurella* Fallén" by de Meijere,

1926: 279). Sønnerup's (1949) records for Denmark were not accepted by Rydén, Lyneborg & Nielsen (1963). Records for Ljungskile, Sweden (Rydén, 1947) and Poland (Nunberg, 1947; Nowakowski, 1954) are also doubtful, as they were based on mines on *Angelica sylvestris* L. Such records could well be due to confusion with mines of *angelicastris*.

*Remarks.* — This species is very close to *Phytomyza selini* Hering and *P. silai* Hering. Hering originally reported the host-plant as *Angelica sylvestris* L., but later revised his identification to *A. palustris* (Besser) (Hering & Spencer, 1968: 180). The latter plant was stated by Braschnikow (1897) to be the host of an unidentified *Phytomyza* species, whose description can refer to no known *Angelica*-miner other than *angelicivora*.

### Some unclarified or incorrect records

Additional unclarified or incorrect records, not mentioned in the preceding text, are as follows.

1. *Agromyza heraclei* Bouché (1847:143). The description cannot be referred to any known miner of *Heracleum*. I suspect that the flies were associated with incorrect data. I doubt whether Hendel (1936:540) was justified in suggesting that Bouché's species was the same as *Phytomyza spondylii* Robineau-Desvoidy, since flies without the second cross-vein (m-m) would hardly have been placed in *Agromyza*.
2. De Meijere (1941a:26) described larvae obtained by H. Buhr from mines on *Pastinaca sativa* L. in Mecklenburg (Germany). Hering (1957, no. 3587) described the mine as follows.

"Mine begins as short, lower-surface, very shallow channel near a leaf-vein; on upper surface it proceeds directly to the leaf-margin, and follows this for most of its course. The margins of the channel are irregularly sinuate. Faeces in a few widely separated particles. Semicircular slit on upper surface".

The species concerned remains unclarified.

3. Spencer (1969:285) has recorded linear mines on *Pastinaca sativa* L. in Quebec (Canada). Probably these were produced by *Phytomyza pastinacae* Hendel, but no flies were obtained.
4. Sehgal (1971:382) has described a female *Phytomyza* fly bred from linear mines on *Angelica arguta* Nutt. at Blairmore, Alberta. The species concerned cannot be determined until males are obtained.
5. Kuroda (1961: 70) has described *Phytomyza* larvae from linear mines on *Angelica decursiva* Franch. & Savat. in Japan. The identity of this species is still unclarified.
6. Entries nos. 373 and 376 in Hering's (1957) key to miners of *Angelica* should be deleted. They were based on records of Spencer's, who now considers them to be incorrect.
7. Hering (1957, no. 378) has doubtfully referred to *Phytomyza spondylii* Robineau-Desvoidy a linear mine collected by Spencer on *Angelica archangelica* L. at Kew Botanical Gardens, London. I have seen this mine, and think it was produced either by *P. spondylii* Robineau-Desvoidy or by *P. pastinacae* Hendel. There is no initial lower-surface channel (contra Hering, 1957), but only the oviposition scar on the lower surface of the leaf. An identification to species is not possible in the absence of bred flies.

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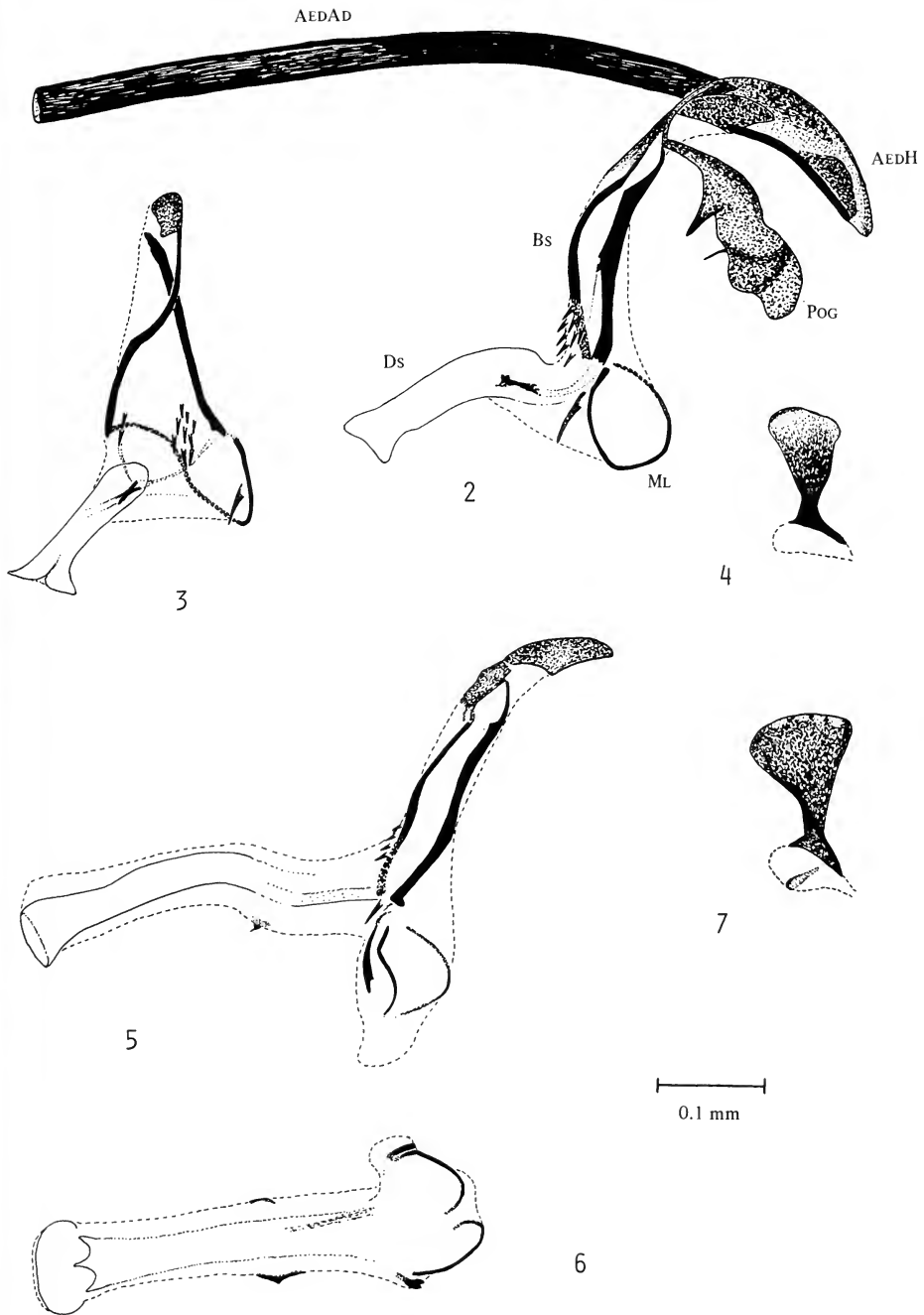


Fig. 2-4. *Phytomyza pastinacae* Hendel (♂), Ireland: 2, aedeagus and associated structures in lateral view (AEDAD aedeagal apodeme, AEDH aedeagal hood, BS basal section of aedeagus, DS distal section of aedeagus, ML medial lobe, POG postgonite); 3, aedeagus in  $\pm$  anterodorsal view; 4, ejaculatory apodeme. Fig. 5-7. *Phytomyza spondylii heracleiphaga* Spencer (♂), Alaska: 5, aedeagus in lateral view; 6, distal section and medial lobe of aedeagus in ventral view; 7, ejaculatory apodeme.

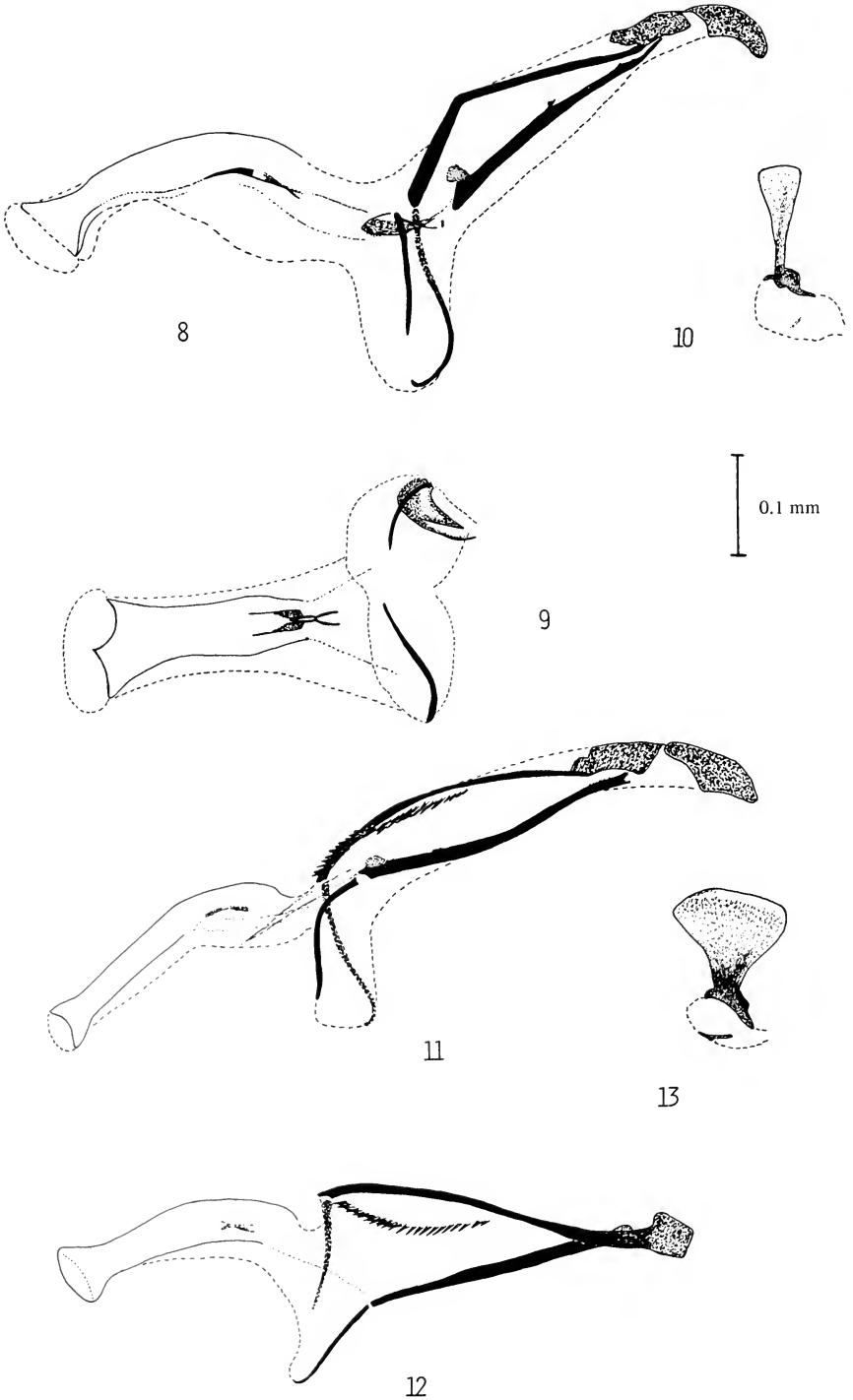


Fig. 8-10. *Phytomyza tlingitica* n. sp., holotype ♂: 8, aedeagus in lateral view; 9, distal section and medial lobe of aedeagus in ventral view; 10, ejaculatory apodeme. Fig. 11-13. *Phytomyza sphondyliivora* Spencer (♂), Surrey, England: 11, aedeagus in lateral view; 12, aedeagus in anterodorsal view; 13, ejaculatory apodeme.

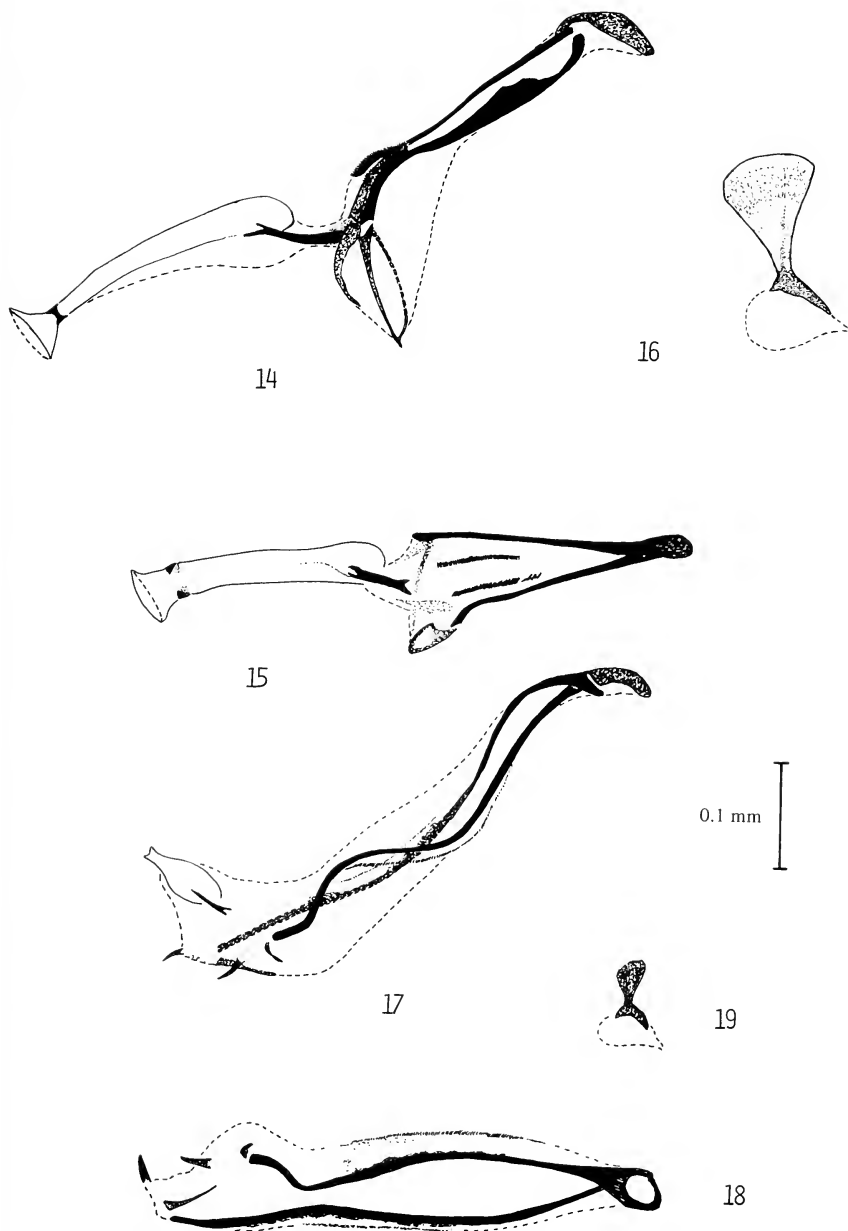


Fig. 14-16. *Phytomyza angelicastris* Hering (♂), München, Germany: 14, aedeagus in lateral view; 15, aedeagus in ± antero-dorsal view; 16, ejaculatory apodeme. Fig. 17-19. *Phytomyza archangelicae* Hering (♂), Alaska: 17, aedeagus in lateral view; 18, basal section of aedeagus (without phallosophore) in ventral view; 19, ejaculatory apodeme.

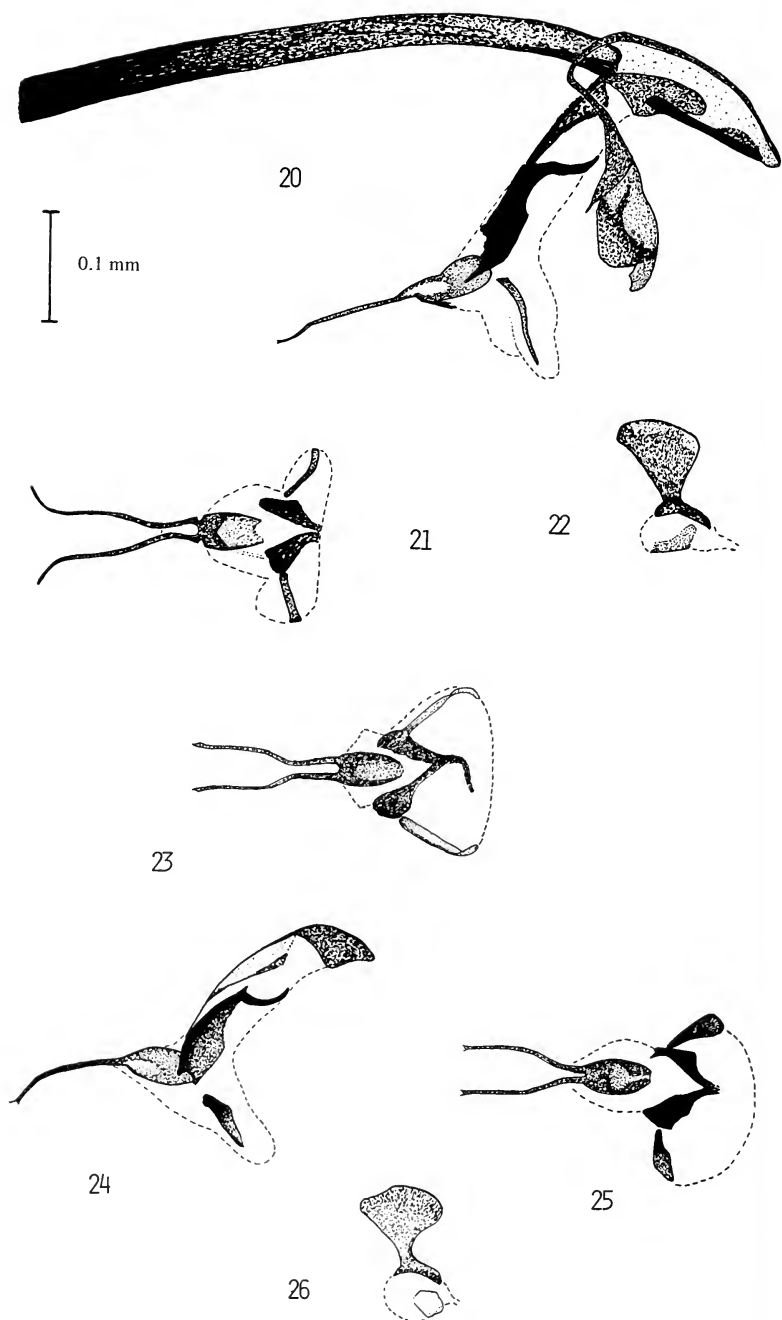


Fig. 20-22. *Phytomyza angelicae* Kaltenbach (♂), Herts., England: 20, aedeagus and associated structures in lateral view; 21, distal section and medial lobe of aedeagus in ventral view; 22, ejaculatory apodeme. Fig. 23. *Phytomyza* sp. ex *Angelica decursiva* Franch. & Savat. (Japan) (♂), distal section and medial lobe of aedeagus in ventral view. Fig. 24-26. *Phytomyza kibunensis* Sasakawa, paratype ♂: 24, aedeagus in lateral view; 25, distal section and medial lobe of aedeagus in ventral view; 26, ejaculatory apodeme.

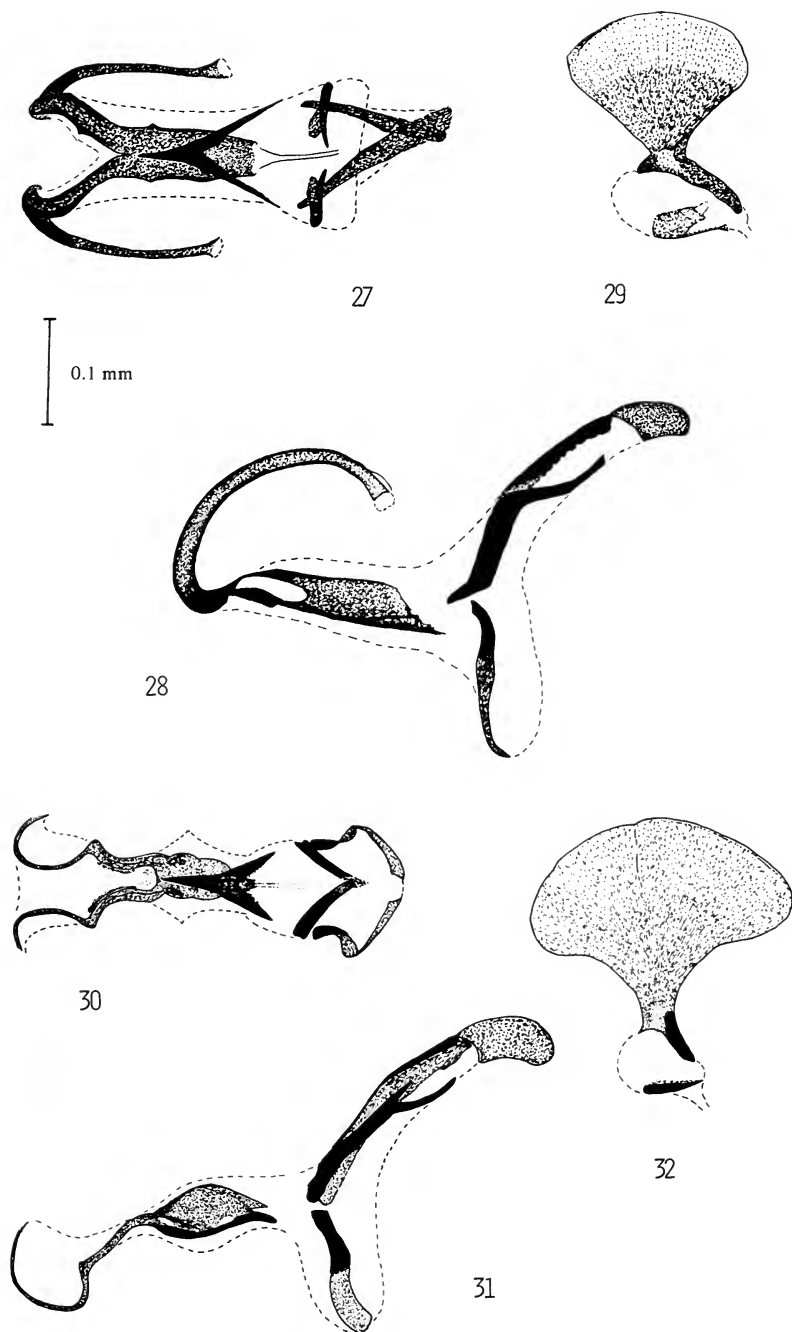


Fig. 27-29. *Phytomyza latifolii* Groschke, holotype ♂: 27, aedeagus in ventral view; 28, aedeagus in lateral view; 29, ejaculatory apodeme. Fig. 30-32. *Phytomyza heracleana* Hering (♂), Berlin, Germany: 30, distal section and medial lobe of aedeagus in ventral view; 31, aedeagus in lateral view; 32, ejaculatory apodeme.

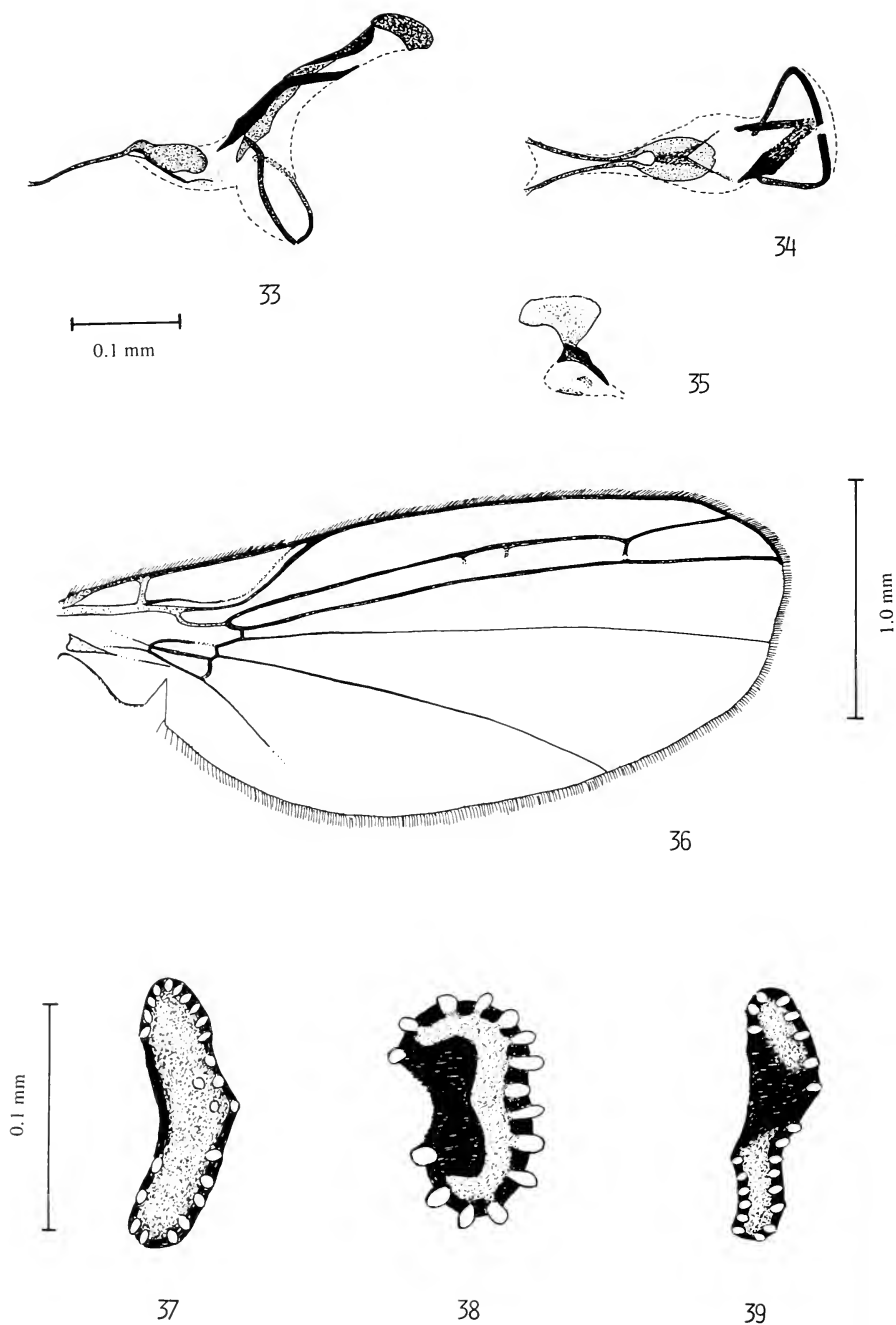


Fig. 33-35. *Phytomyza angelicivora* Hering (♂), Berlin, Germany: 33, aedeagus in lateral view; 34, distal section and medial lobe of aedeagus in ventral view; 35, ejaculatory apodeme. Fig. 36. Wing of *Phytomyza tlingitica* n. sp. (paratype ♀), showing cross-veins between  $r_2 + 3$  and  $r_4 + 5$  and truncate wing tip. Fig. 37. *Phytomyza angelicastro* Hering (England), posterior spiracle of puparium in caudal view. Fig. 38. *Phytomyza angelicae* Kaltenbach (Germany), posterior spiracle of puparium in caudal view. Fig. 39. *Phytomyza archangelicae* Hering (Alaska), posterior spiracle of puparium in caudal view.

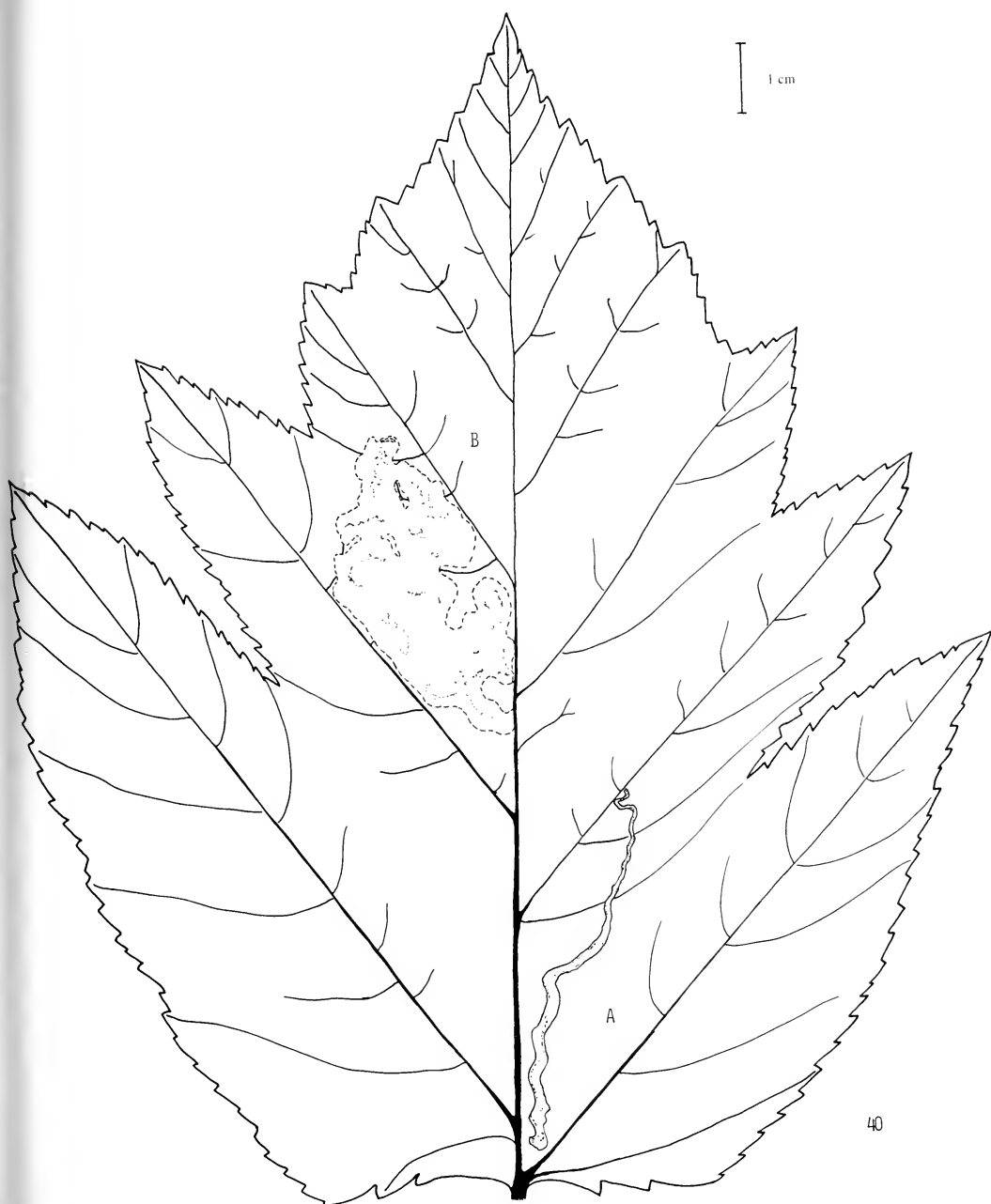


Fig. 40. Leaf of *Heracleum lanatum* Michx. with mines of *Phytomyza spondylii heracleiphaga* Spencer (A) and *P. tlingitica* n. sp. (B).

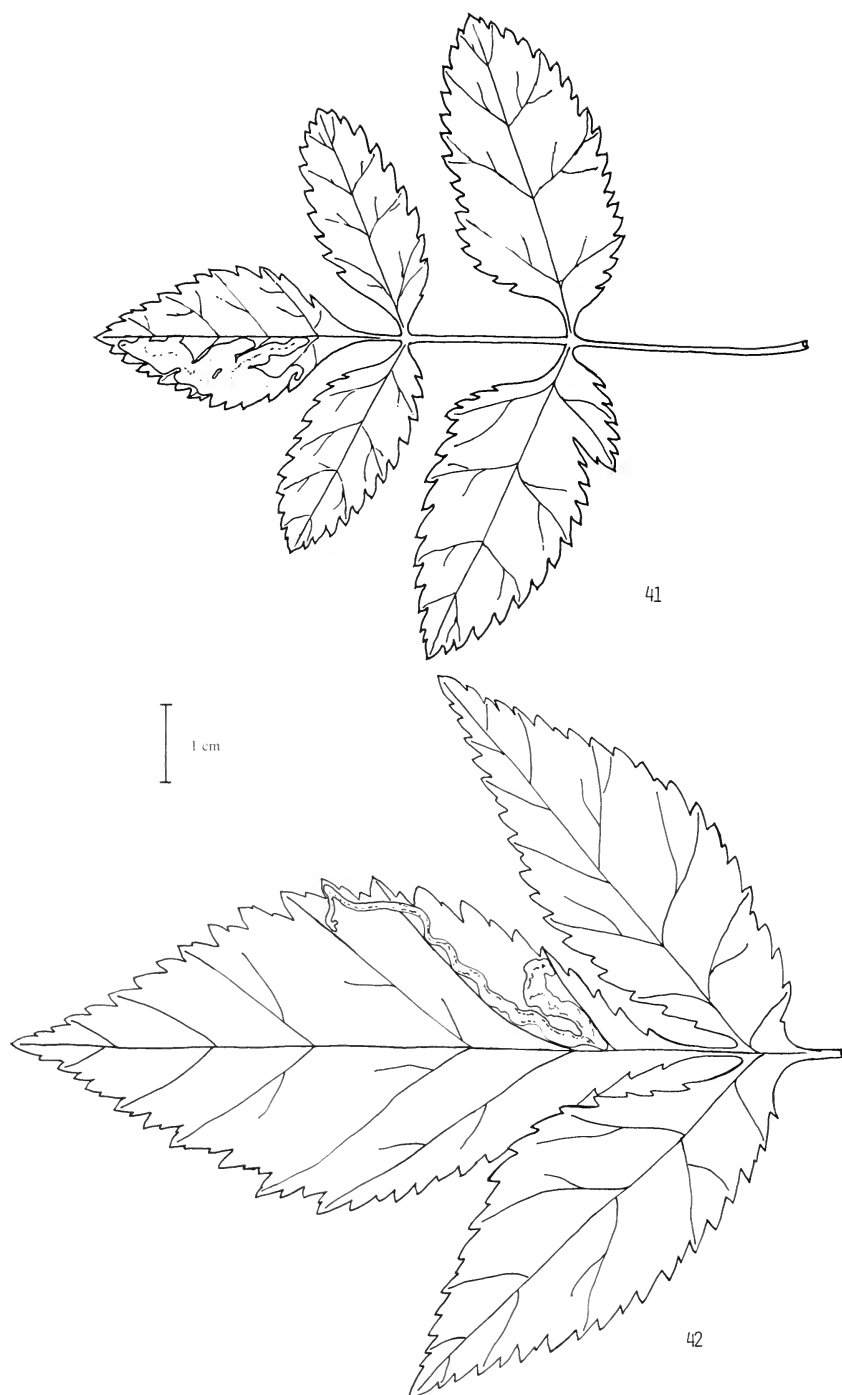


Fig. 41. Leaf of *Angelica sylvestris* L. with mine of *Phytomyza angelicastris* Hering. Fig. 42. Leaflet of *Angelica genusflexa* Nutt. with mine of *Phytomyza archangelicae* Hering.



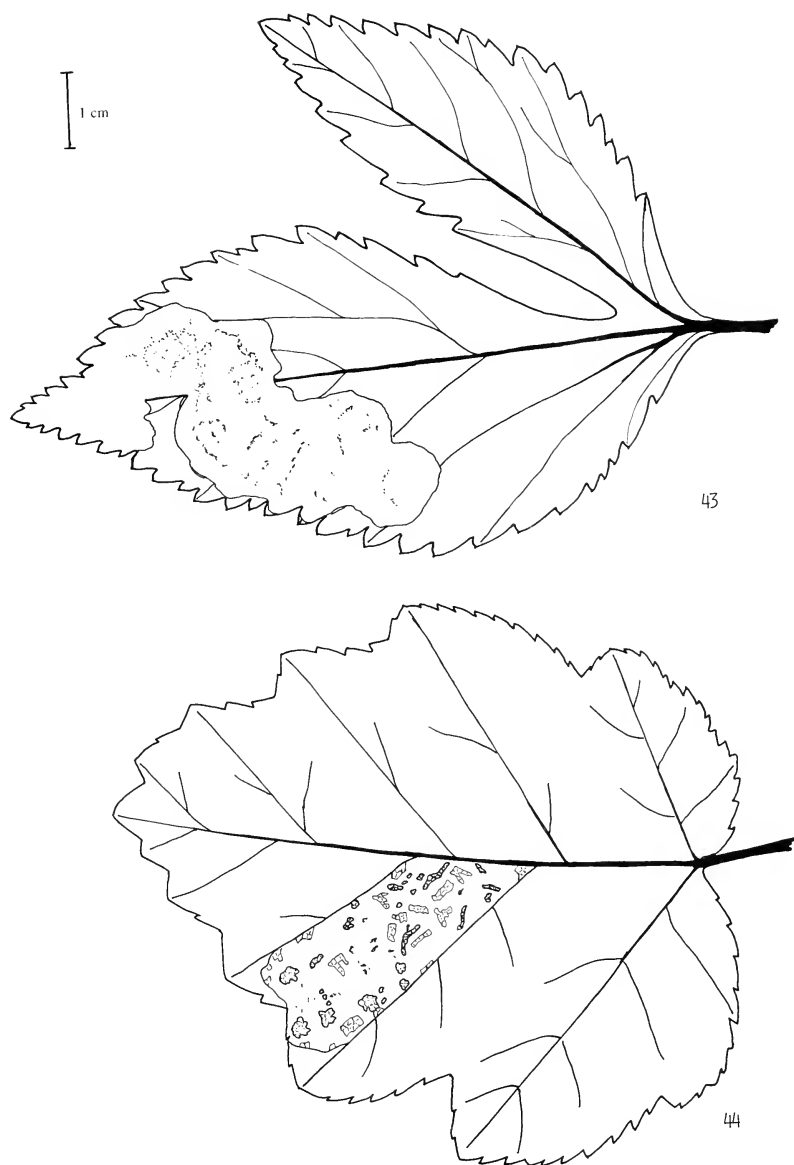


Fig. 43. Leaflet of *Angelica lucida* L. with communal mine of *Phytomyza angelicae* Kalténbach. Fig. 44. Leaf of *Heracleum sphondylium* L. with mine of *Phytomyza heracleana* Hering.

## Book Review

LINDNER, E. 1973. Alpenfliegen. Goecke & Evers, Krefeld. 204 pp., 135 figures (including one colour plate). Size 16 x 24 cm., hard covers. Price: 66 DM (about \$27 Canadian at May 1973 exchange rates, after addition of postage, packing and bank charges).

Professor Dr. Erwin Lindner has become a father figure to modern Dipterists. Back in the 'twenties he founded the well-known series "Die Fliegen der paläarktischen Region", of which he is still the editor. Now long past normal retirement age, he works on at the Staatliches Museum für Naturkunde in Stuttgart, where he holds the rank of Chief Curator (Hauptkonservator i.R.). His new book on alpine flies is the result of over half a century of field work.

As readers of this book Lindner has in mind mainly the many naturalists who visit the Alps. The longest part of the book consists of description and discussion of about 100 selected species. The descriptions are detailed, of a standard appropriate to taxonomic works. The families treated in most detail are the Blepharoceridae (on the basis mainly of Mannheim's work), Tipulidae, Stratiomyidae, Rhagionidae, Acroceridae, Asilidae, Empididae, Syrphidae, Psilidae, Satophagidae, Muscidae, Anthomyiidae and Tachinidae. Canadian students of these families will find Lindner's book helpful, as some of the species treated are holarctic and most have close relatives here. The introductory sections to the book include some entitled "The history of investigation of alpine Diptera", "Biocenoses in the Alps", "Diagnostic characters of nival Diptera", "Boreoalpine glacial relics", "Biological altitude-zones in the Alps" and "Massifs de refuge".

The book is well illustrated, mostly with line and wash drawings but including also a colour plate of the Muscid *Mesembrina mystacea* (L.). Some of the drawings are original, others copies (mostly from "Die Fliegen der paläarktischen Region" and a dissertation on Blepharoceridae by B. J. Mannheim). I noted only one printing error of consequence ("*Gymnocera*" for "*Gymnomera*" in the caption to Fig. 78).

The book has certain limitations. The author has been highly selective in what he has treated, presumably to contain the size and price of the book. I would have liked to see included more information on high altitude Chironomidae and a summary of Groschke's work on alpine Agromyzidae. It would also have been useful if lists of references had been given under each family, for the benefit of readers who wish to pursue their interests further. However, such omissions do not detract from the fact that the information presented is reliable and interesting. I can sincerely recommend the book to all who wish to afford it. It is a pity the price is so high as a result of recent changes in exchange rates.

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## Book Review

ZUMPT, F. 1973. The Stomoxyine Biting Flies of the World (Diptera: Muscidae): Taxonomy, biology, economic importance and control measures. Gustav Fischer Verlag, Stuttgart. viii + 175 pp., 97 figs., 451 refs. Price DM98.

This book, "a summarizing treatise for the entomological, veterinary and medical professions" is the fruit of a project begun in 1938. Opening chapters deal with general morphology and anatomy, and classification of the ten genera. A systematic catalogue and keys to genera and species are included; I found the keys easy to use.

The greater part of the book consists of notes on the taxonomy and biology of the 47 known species, including two new descriptions from the Ethiopian region *Parastomoxys mossambica* and *Prostomoxys saegerae*. The usual stomoxyine mode of life is a close association with large ungulates, the adult flies sucking blood or feeding on sores and the larvae developing in the dung. The most widespread of the synanthropic species, the stable fly *Stomoxys calcitrans* (L.), is more catholic in its tastes, developing not only in dung, but also in decaying vegetables, seaweed and even, by the Tennessee river, on the accumulated dead bodies of mayflies. A more aberrant form of development may be followed by *S. ochrosoma* Speiser which has been found only near columns of army ants (Dorylinae) in East Africa. Thrope once observed a female hovering over a column and dropping a whitish object, possibly an egg which was borne off by a worker to develop, he suggested, in the bivouac. Unfortunately this observation has never been repeated.

*Stomoxys* bites are intensely irritating. They have been shown to cause reduction of milk yield in cattle, and even to drive lions from their territories. However, there are no reliable records of severe toxic reactions, such as are known from the bites of *Simulium*. The author, himself a world authority on myiasis, dismisses the few reports of Stomoxyine myiasis as accidental or pseudomyiasis.

Certain Stomoxyinae have been incriminated in mechanical transmission of human diseases and in both mechanical and cyclical transmission of diseases of other animals. Animal pathogens transmitted include: *Habronema*, an enteric nematode of horses; *Trypanosoma evansi* the causal agent of surra in camels, horses, and other animals; and *Brucella abortus* of cattle, which may also be transmitted to man. Early reports of the transmission of human poliomyelitis by *S. calcitrans* have been rejected by later workers.

Actual and potential control measures are discussed. Various insecticidal treatments are widely used for the control of the horn fly, *Haematobia irritans* (L.). Stable fly larvae may be controlled without resort to insecticides simply by drying the dung before the larvae can pupate. Scarabaeid beetles have proved helpful in this respect; their tunnelling dries the dung and exposes the larvae to predation by ants. One of the most complete studies of parasitism of horn fly pupae by Hymenoptera is Depner's in Southern Alberta. He concluded that the parasites kept down hornfly populations in the parkland and foothills but not on the prairies. It may be possible to control *S. calcitrans* by sterile males since its populations are focal and the females mate only once, but this method has not yet been put into practice.

The concluding chapter gives notes on methods of collection, preservation, and cultivation of Stomoxyinae.

This book will be a valuable reference work. However, it could have been made easier for non-dipterists to use if the orientation of the male terminalia (figs. 9 and 10) in the intact

fly had been indicated. Fig. 9 seems to be a postero-ventral view of the tip of the abdomen, but the orientation of the disarticulated parts in Fig. 10 is not clear to me.

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### Book Review

WEHNER, R. (Editor). 1972. Information processing in the visual systems of Arthropods. Springer, Berlin, New York. xi+334 pp., 263 figs., paperback. \$11.50 (U.S.)

This book is the proceedings of a symposium held 6-9 March 1972 at the Department of Zoology, University of Zurich, designed to summarize structure and function of the compound eye of selected arthropods, and to apply this knowledge to the performance of the visual system in colour discrimination, pattern recognition, and other central nervous processes. Included are: preface, contents, list of participants (77), opening remarks, and 45 papers arranged in 9 parts. There is no index.

In Part 1, "Anatomy of the visual system", the structure of the ommatidium of *Musca domestica* is summarized; details of the first visual ganglion and cartridges of the lamina are given and three mechanisms of movement detection are proposed (Braitenberg). The types of neuronal elements and synapses in the optical cartridge are documented by Boschek. Strausfeld and Campos-Ortega explain the complex arrangement of feed-back and feed-forward loops. Menzel details the fine structure and pigment migrations of apposition eyes of *Formica polyctena*. The orientation of the microvilli of the eight retinula cells of the eyes of *Cataglyphis bicolor* are examined by Herrling. Expertly, Paulus describes the completely irregular, radially symmetrical, and bilaterally symmetrical rhabdoms of the eucone ommatidia of Collembola.

In Part 2, "Optics of the compound eye", Kirschfeld documents the concept of "neural superposition" via optomotor experimentation in the unfused rhabdomeres of *Musca domestica*. From rapid pigment migration studies in light adapting *Drosophila* eyes, Franceschini explains the "deep pseudopupil" seen in this and other insects. Gaussian curves are derived from continuous light intensity distributions in single fused rhabdoms of *Apis mellifera* (Eheim). Observations through the cornea of transparent mutants of *Ephesia kühniella* and *Chrysopa vulgaris*, provide Kunze with the data for superposition eye glow via pigment migrations from the edges to the centre of the facet. An inverted image of a microneedle is viewed through the cornea. Hengstenberg measures "clock-spikes" produced by a motoneuron in the subesophageal ganglion of *Musca domestica*.

"Biochemistry of visual pigments" is discussed in Part 3. Using various Insecta, and Mollusca, Hamdorf and Langer describe spectrophotometric measurements of the sequence of the absorption of a light quantum by a rhodopsin molecule through the short-lived intermediate prelumi- and lumirhodopsin to metarhodopsin, which has a longer life span and enters into a pH-dependent equilibrium with the UV-absorbing metarhodopsin II.

Part 4 summarizes experimental results postulated from, "Intensity-dependent reactions". Biophysics of the discrimination of light intensities of *Apis mellifera* (Labhart) and photo-positive reactions to circular areas (Frischknecht) are described. Stationary flight thrust reduction as a function of luminance can be elicited throughout the visual field by direct stimulation of the visual elements of *Drosophila* and *Musca* (Buchner).

"Wavelength-dependent reactions" are the cohesive topic of Part 5. Burkhardt and de la Motte conducted comparative ERG studies of light sensitivity (Hymenoptera) and spectral response curves (Diptera, Mecoptera). Intensity discrimination of *Drosophila melanogaster* increases in the presence of UV light (Schuemperli). Kaiser and Liske conclude that *Apis mellifera* has no colour-specific optomotor reactions, but a highly contrast-sensitive optomotor system. Colour senses of various Insecta are determined by spectral sensitivity and wavelength discrimination (Toggweiler, Roth, Menzel).

In the sixth part, "Pattern recognition", the possibilities of correlations between neurophysiology and behaviour are investigated. Using *Apis mellifica* (= *A. mellifera*) and *Cataglyphis bicolor*, Wehner analyzes pattern detection and modulation measurements utilizing the light flux of a single rhabdom. Cruse researches the coefficient of the correlation function of two dimensional pattern discrimination by *Apis mellifera*. Bees cannot form a concept of "triangularity" (Anderson). Land reviews the anatomy and optics of Salticid spiders. Vision angle determination, overlap of adjoining ommatidia, and orientation of the microvilli of the rhabdoms of Collembola are documented by Schaller.

"Visual control of orientation patterns" is the theme of Part 7. In an attempt to divide the visual system into physiological constituents, Heisenberg analyzes behavioural diagnostics of *Drosophila* visual mutants including: ERG defect, optomotor response, and polarization sensitivity. Retreat along a horizontal web by *Agelena labyrinthica* Clerck is discussed by Goerner to determine the interdependency of optical and kinesthetic orientation. Idiothetic course control and visual orientation in Orthoptera are determined by statistical analysis (Mittelstaedt-Burger). Anemomenotactic orientation mechanisms are employed from 1-350 lux; astromenotactic mechanisms function beyond 350 lux (Duelli) utilizing the middle and frontal regions of the *cataglyphis bicolor* eye (Weiler & Huber). Terrestrial clues are also employed in distance measuring mechanisms (Wehner, Flatt, Burkhalter).

In Part 8, "Storage of visual information", Erber reports experiments with the learning behaviour of *Apis mellifera* and the dependence parameters: "quantity and duration of reward". Masuhr and Menzel conclude that the visual system is responsible for long distance orientation.

Helverson provides a mathematical discussion of the bee's mechanism of translation of the difference between two stimuli in Part 9, "Methods of quantifying behavioural data". The curve of the relationship between "perceived stimulus" and "choice frequency" is sigmoid.

Like most symposium proceedings this is by no means a complete coverage of the visual system of Arthropoda, or even of the field suggested by the title, though it covers much beyond this. It does document recent European experimentation and emphasizes the neurophysiological advantages of the arthropod systems. Papers from North America or earlier than the mid sixties are rarely cited. Because of the diversity of specificity, the publication is saltatory. Graphs, charts, diagrams, and micrographs are numerous but some are too small. Generic and specific names are neither italicized nor underscored. These minor oversights are probably the result of the rapid publication of the text, only three months following the symposium.

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## Entomological Society of Canada Writing Prize, 1973

To encourage people to enter the field of "popular science" writing, the Entomological Society of Canada is offering three prizes, one of \$500 and two of \$250 each, for good popular articles on entomological subjects. Five additional prizes of \$100 each are being provided by *Insect World Digest* for five runners-up.

Entries will be expected to show the beauty, intricacy, and interest of the insect world to the non-scientist. Attractive illustrations, color photographs and subjects that demonstrate relationships between insects and man may be advantageous, but each entry will be judged on its own merits with regard to literary style, scientific accuracy and general interest. Entries should be of a quality acceptable to widely-read magazines and journals.

As a condition of entry authors will assign all rights to prize-winning articles to the Entomological Society of Canada. All other entries will be returned to the authors after judging is complete, provided that they are accompanied by a self-addressed envelope and return postage (Canadian stamps or international reply coupon).

The eight prize-winning articles will be published by *Insect World Digest* within twelve months of announcement of the awards, without additional payment to the authors. Other entries will be reviewed by *Insect World Digest* with a view to publication and payment at their regular rates, subject to direct negotiation with the authors.

The Entomological Society of Canada may submit prize-winning articles to other magazines or journals after they have appeared in *Insect World Digest*. The proceeds from these and any other sales will be divided between the authors (70%) and the Entomological Society (30%).

Entries will be judged by a committee appointed by the Entomological Society of Canada. The decisions of the committee will be final and prizes will be awarded only to entries of satisfactory quality.

To be eligible an entrant must be either a resident of Canada or a member of the Entomological Society of Canada. Entry forms may be obtained from

K. S. McKinlay,  
Agriculture Canada Research Station,  
University Campus,  
Saskatoon, Sask. S7N 0X2

and entries must be despatched to reach that address by December 31, 1973.

Biting Fly Control and Environmental Quality — Proceedings of a Symposium  
held at the University of Alberta in Edmonton, May 16, 17, and 18, 1972.

The proceedings of this symposium, which was organized jointly by the Department of Entomology at the University of Alberta and the Advisory Committee on Entomology of the Defence Research Board, have been published. The proceedings are available and have been distributed to participants. Extra copies are available to participants and others at \$2.00. It will save mailing costs, office work and bookkeeping if, wherever possible, orders from an institution are consolidated and if payment could be included with orders. Orders should be addressed to the Department of Entomology, University of Alberta, Edmonton, Canada T6G 2E3.





Publication of *Quaestiones Entomologicae* was started in 1965 as part of a memorial project for Professor E. H. Strickland, the founder of the Department of Entomology at the University of Alberta in Edmonton in 1922.

It is intended to provide prompt low-cost publication for accounts of entomological research of greater than average length, with priority given to work in Professor Strickland's special fields of interest including entomology in Alberta, systematic work, and other papers based on work done at the University of Alberta.

Copy should conform to the Style Manual for Biological Journals published by the American Institute of Biological Sciences, Second Edition, 1964, except as regards the abbreviations of titles of periodicals which should be those given in the World List of Scientific Periodicals, 1964 Edition. The appropriate abbreviation for this journal is *Quaest. ent.* An abstract of not more than 500 words is required. All manuscripts will be reviewed by referees.

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A periodical record of entomological investigations,  
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University of Alberta, Edmonton, Canada.

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## Book Review

HODEK, I., et al. 1973. Biology of Coccinellidae. Academia, Czechoslovak Academy of Sciences, Prague. Hard covers, size 7" x 11", 260 pages, 34 plates (16 in color), 58 photographs, classified index, 517 references. Price: \$41.00 U.S., from Dr. W. Junk Publishers, The Hague, Netherlands.

Aside from gradual accumulation of new knowledge about ladybird beetles, the study of Coccinellidae has enjoyed a resurgence of interest among coleopterists as well as ecologists. The failure of insecticides to control some economically important insect pests has accelerated developments in the field of biological control as a necessary alternative. The predaceous group of coccinellid beetles was intensively studied for its potential in biological control of coccids, mites and aphids. Unfortunately, only the coccid feeding species proved to be of practical value. On the other hand, the plant feeding members of this family, e.g. *Epilachna* spp., are highly destructive pests to leguminose and cucurbitaceous plantations (beans, squash).

The voluminous literature on predaceous Coccinellidae was previously reviewed by Hagen (1962) and Hodek (1967) in the Annual Review of Entomology, and the present volume is in effect an updated and enlarged version of these two earlier review articles. Similar to the Annual Review in its style and form, the literature is treated in the following nine subject categories (number of pages for each is indicated in brackets): taxonomy and morphology of adults (9); morphology and taxonomy of larvae with keys for their identification (16); variability and genetic studies (11); life history and biological properties (5); distribution in habitats (18); food relations (28); dormancy (34); enemies of Coccinellidae (15); effectiveness and utilization (17). Approximately one half of the text is occupied by graphs, figures, *et cetera* to illustrate the highlights of discussion.

Of the 19 color plates, the first three are a pictorial key to selected Palaearctic coccinellid larvae. This section is also supplied separately with the book for field use. The remaining 16 plates illustrate dorsal aspects of immature stages of some Palaearctic Coccinellidae, (4th instar larvae and pupae).

Hodek's "Biology of Coccinellidae" treats only the predaceous coccinellids with emphasis on studies of diapause. Much of the discussion is concentrated on Palaearctic species. One wonders for how many more years undue emphasis will be given to studies of the common European *Coccinella septempunctata* Linnaeus. The section on taxonomy is in general inadequate. Many significant references have been omitted.

The title of the book is pretentious, for it implies coverage of a more comprehensive body of information than is actually included. Much of the text has been borrowed directly or slightly modified from original sources. The information presented is not suf-

ficiently integrated or synthesized so the text is disjointed. At the back of the book are 58 photographs many of which are of questionable value because they are technically poor or illustrate insignificant information. These deficiencies as well as syntactic and semantic errors could have been eliminated by careful editing.

The colored illustrations do not redeem the book. Thus, the price, which under ordinary circumstances might be regarded as only unreasonably high, seems outrageously high. Most of the information can be obtained from the articles in the Annual Reviews of Entomology, referred to above. Xerox copies of them could be obtained for a quarter of the price of Hodek's book. Wealthy entomological bibliophiles might want to purchase the latter item.

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## Book Review

HABU, A. 1973. Fauna Japonica. Carabidae. Harpalini (Insecta Coleoptera). Keigau Publishing Company, Hagiwara Building, 3-1, 2-chome Sarugaku-cho, Chiyoda-ku, Tokyo, Japan. xiii + 430 pages, 782 test figures, plates I-IV (colored), plates V-XXIV (black and white). Price \$50.00 USA.

This volume describes in English the harpaline fauna of Japan including adults of 101 species arrayed in 17 genera and 4 subtribes, and larvae of 28 species representing 7 genera. Keys are provided at appropriate places in the text to adults of all taxa. The known larvae are treated in a single key near the beginning of the volume.

Each taxon is adequately described to allow identification of its members, a task eased by illustrations of habitus provided in the plates, and by text figures which illustrate various structures including mouthparts, legs, ovipositors and male genitalia. Japanese vernacular names are given for each species. General distribution of each species and type localities of new species are indicated. For many species notes are included about food habits and life history. For genera and subgenera type species are listed. Synonymies and abbreviated literature citations are presented in the text, and complete citations in the "Literature" section. An index to scientific and vernacular names follows the text.

The illustrations are excellent, and the artist who prepared the colored illustrations, Mr. T. Sekiguchi is to be congratulated for the high quality of his work. However, it would be desirable to include with each some indication of the size of the figured insect. The paper, printing and binding are of the same high quality which characterizes the earlier volumes in this series. However, the overall excellence of the work is marred by spelling errors most of which could have been avoided had the manuscript and proofs been read by an entomologist whose native language is English.

The taxonomic treatment is conservative and sound. This work can be easily integrated with recently published treatments of geographically more or less adjacent harpaline faunas: Darlington (1968, The Carabidae of New Guinea, Part III, Bull. Mus. Comp. Zool., 137: 1-253) and Lindroth (1968, The ground-beetles of Canada and Alaska, Part 5, Opuscula Entomologica, Supplementum XXXIII, pp. 649-944). No new genera are described and the few new subgenera seem well founded, each on a distinctive combination of several character states. The subgeneric category is consistently used, and in the more diverse genera the "species group" is used as an infrasubgeneric category.

This volume is an annotated catalogue, useful for identification and as a compendium of biological information about Japanese harpalines. However, the author makes no effort to analyze his data in terms of phylogenetic or biogeographic theory, nor does he contribute much to harpaline classification, beyond brief reference to his reasons for combining the genus-groups Harpali and Selenophori. For the student of carabids and for the general student of diversity interested in acquiring an understanding of the Japanese fauna, maps of species ranges would have been useful and informative, and for the student of harpaline classification drawings of the everted internal sacs of the male genitalia would have provided much sorely needed data. This is especially true for the genus *Harpalus*. Lindroth (cited above) showed the value of the armature of the internal sac as a tool in classification. It would have been interesting to compare with Lindroth's treatment of North American *Harpalus*, a similar study of the Japanese species of this genus. In this connection, one valuable point made by Habu relates to the possible over-emphasis placed by Jeannel and Lindroth on the position of the apical orifice of the male median lobe. The latter authors include in *Harpalus* only those species with the apical orifice left-lateral in position. Habu does not give special weight to this feature, and includes also in *Harpalus* species with the apical orifice dorsal in position. Careful evaluation of these conflicting viewpoints will be

required by future workers on classification of *Harpalus*.

Of special interest to the student of historical zoogeography would be the genus *Trichotichnus*, represented in Japan by 27 species, 24 of which seem to be endemic. The latter number represents nearly half of the total harpaline species confined to these islands. Data obtained from the distribution patterns and relationships of the *Trichotichnus* species might be informative about the history of the Japanese biota when linked to data about Pleistocene climatic events, past inter-island connections and island-mainland connections.

Vestiture of the male front tarsus provides for the Japanese fauna, as for all other faunas to date, the best diagnostic character to distinguish between the subtribes Anisodactylina and Harpalina. Thus, it is troublesome to identify females not associated with males. A second troublesome detail which emerges from examination of Habu's identification systems is the sequence in which the larvae key out. Their diagnostic characteristics do not seem to indicate the same groupings as do the adult characteristics, and this suggests that larval characters might be of limited value in improving classification of the Harpalini. These points are not criticisms of this volume. Rather, they indicate difficulties inherent in working with harpaline carabids.

The subject of geographical variation, of great interest to students of diversity, was seemingly ignored except for an effectively illustrated treatment of *Platymetopus flavilabris*, based on samples from localities throughout the range of this Oriental-eastern Palaearctic species.

In spite of the high cost of this volume and coverage in general being restricted to simple descriptive statements, its technical excellence commends it to general coleopterists interested in the Asiatic fauna as well as to carabid specialists. Dr. Habu is to be congratulated for presenting such a fine study of one of the more complex and difficult groups of carabid beetles. He is also to be thanked for writing in English by those, such as myself, whose limited reading abilities confine us to the literature of a few Indo-European languages.

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*Anisodactylus (Pseudaplocentrus) laetus* Dejean. Lake Chicot State Park, Louisiana (body length of specimen 8.5 mm.).  
Photograph by J. Scott.

THE ANISODACTYLINES (INSECTA:COLEOPTERA:CARABIDAE:  
HARPALINI): CLASSIFICATION, EVOLUTION, AND ZOOGEOGRAPHY

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Quaestiones entomologicae

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*The North American species of Anisotarsus Chaudoir, Notiobia (s. str.) Perty, and Gynandrotarsus LaFerté together with all supra-specific taxa of the subtribe Anisodactylina are revised. Keys and descriptions are provided to revised species and all supra-specific taxa. Morphological characters useful in distinguishing taxa are discussed and illustrated. Synonyms of revised taxa are listed and reasons for regarding them as synonyms discussed. Where necessary, lectotypes, neotypes, and type species are designated. The distribution of each revised species is described in the text and also illustrated by a map. Geographical and intrapopulational variation of the revised species are analyzed, and available information on flight and bionomics is also presented.*

*The genus-group taxa Notiobia (s. str.) and Anisotarsus are treated as subgenera of Notiobia (s. lat.). Thirteen species are recognized in the subgenus Anisotarsus; one of these, schlingeri (type locality 12.4 mi. s. Tecalitlan, Jalisco, Mexico) is new. Ten species are recognized in the subgenus Notiobia with cooperi (type locality Tepic, Nayarit, Mexico) and ewarti (type locality Coyame, Lake Catemaco, Veracruz, Mexico) being new species. The subgenus Gynandrotarsus (genus Anisodactylus) is considered to have 10 valid species, including a new one, darlingtoni (type locality e. of Morelia on Rte. 15, Michoacan, Mexico).*

*Thirty-seven genera and subgenera and 24 genera are regarded as members of Anisodactylina. Three of the 37 genera and subgenera are new: the genus Pseudanisotarsus (type species Anisotarsus nicki van Emden, 1953); and the subgenera Pseudanisodactylus (type species Anisodactylus punctatipennis Morawitz, 1862) and Pseudaplocentrus (type species Anisodactylus laetus Dejean, 1829) of the genus Anisodactylus. The subgeneric name "Pseudhexatrichus" (genus Anisodactylus) is validated with Anisodactylus dejeani Buquet, 1840 designated as type species. Progonochaetus basilewskyi is proposed as a replacement name for Dichaetochilus jeanneli Basilewsky, 1946 because both D. jeanneli Basilewsky, 1946 and Rasnodactylus jeanneli Basilewsky, 1946 are regarded as members of the genus Progonochaetus.*

*The phylogenies of the supra-specific taxa and revised species of Anisotarsus and Gynandrotarsus are reconstructed by cladistic techniques slightly modified from those proposed by Hennig. Analysis of the supra-specific reconstructed phylogeny indicates: that primitive taxa are concentrated in the Australian Region with more derived ones concentrated in the Northern Hemisphere; and that now widely separated continents such as Africa and South America contain "sister" taxa (sensu Hennig). It is postulated that the Anisodactylines evolved on the combined continents of Australia and Antarctica during late Jurassic or early Cretaceous and dispersed northward during phases of continental drift. The zoogeography of the genera and subgenera of Anisodactylina is discussed in detail.*

*Study of the reconstructed phylogeny of North American species of Anisotarsus and examination of South American species suggest that the North American species are derived from 2 separate invasions of South American ancestors. Present North American species distributions are studied and explained by reference to past North American climatic, geological, faunal, and floral changes.*

*Since the closest cladistic relatives of many North American species of Notiobia (s. str.)*

seem to be Middle or South American forms which are poorly known, it is concluded that reconstruction of the phylogeny of North American species must be deferred.

The closest cladistic relative of *Gynandrotarsus* is *Pseudodichirus* which is the more primitive of the 2 groups and is found in Europe. It is postulated that the ancestor of *Gynandrotarsus* crossed from Europe to North America during very late Cretaceous or early Tertiary via the then broad land connection between Europe and eastern North America. Present species distributions are studied and explained by reference to past North American climatic, geological, faunal and floral changes.

*Les espèces nord-américaines d'Anisotarsus Chaudoir, Notiobia (s. str.) Perty et Gynandrotarsus LaFerté et tous les taxa supragénériques de la sous-tribu Anisodactylina sont revus. Des clefs et des descriptions sont pourvues pour les espèces revues et pour tout taxa supra-spécifiques. Tout caractère morphologique jugé utile est discuté et illustré. Une liste des synonymes est pourvue, et chaque cas est discuté. Lorsque nécessaire, les lectotypes, les néotypes et les espèces type sont désignés. La distribution géographique de chaque espèce revue est décrite dans le texte et illustré par une carte géographique. Les variations géographiques et les variations à l'intérieur des populations est analysées pour les espèces revues, et lorsque l'information est disponible les données sur le vol et la bionomie sont présentées.*

*Les genres Notiobia (s. str.) et Anisotarsus sont traités comme sous-genres des Notiobia (s. lat.). Treize espèces sont reconnues dans le sous-genre Anisotarsus; l'une d'elle est nouvelle, schlingeri (localité type 12.4 mi. s. Tecalitlan, Jalisco, Mexico). Dix espèces sont reconnues dans le sous-genre Notiobia avec cooperi (localité type Tepic, Nayarit, Mexico) et ewarti (localité type Coyame, lake Catemaco, Veracruz, Mexico) comme espèces nouvelles.*

*Trente-sept genres et sous-genres, et 24 genres sont reconnus comme membres des Anisodactylina. Trois d'entre eux sont nouveaux: le genre Pseudanisotarsus (espèce type Anisotarsus nicki van Emden, 1953); et dans le genre Anisodactylus les sous-genres Pseudanisodactylus (Espèce type Anisodactylus punctatipennis Morawitz, 1862) et Pseudaplocentrus (espèce type Anisodactylus laetus Dejean, 1829). Le nom sous-générique "Pseudhexatrichus" du genre Anisodactylus est valide, et l'Anisodactylus dejeani Buquet, 1840 est désigné comme l'espèce type. Progonochaetus basilewski est proposé comme un nom de remplacement pour Dichaetochilus jeanneli Basilewsky, 1946 car D. jeanneli Basilewsky, 1946, et Rasnodactylus jeanneli Basilewsky, 1946 sont considérés comme membres du genre Progonochaetus.*

*Les phylogénies des taxa supra-spécifiques et des espèces d'Anisotarsus et de Gynandrotarsus sont reconstruites au moyen de techniques cladistiques légèrement modifiées de celles proposées par Hennig. L'analyse de la phylogénie reconstruite pour les taxa supra-spécifiques indique que les taxa primitifs sont concentrés dans la région Australienne, que les plus évolués sont concentrés dans l'hémisphère nord, et que l'Afrique et l'Amérique du sud, malgré les grandes distances entre elles, contiennent présentement des taxa soeurs. Il est postulé que les Anisodactylines ont évolué sur les continents combinés d'Australie et d'Antarctique à la fin du Jurassique ou au début du Crétacé, et plus tard ils se dispersèrent vers le nord durant les phases de la dérive continentale. La zoogéographie des genres et sous-genres des Anisodactylina est discutée en détail.*

*L'étude de la phylogénie reconstruite des espèces d'Anisotarsus nord américains et l'examination des espèces sud américaines suggèrent que les espèces nord américaines sont originées lors de deux invasions d'ancêtres sud américains. La distribution présente des espèces nord américaines sont étudiée et expliquée en relation aux anciens climats, et changements géologiques, faunistiques et floristiques en Amérique du nord.*

Comme les espèces les plus voisines cladistiquement de plusieurs espèces nord américaines de *Notiobia* (s. str.) semblent appartenir à des formes peu connues l'Ameriques central et d'Amérique du sud, il est conclu. que la reconstruction de la phylogénie des espèces nord américaines doit être remise à plus tard.

Le sous-genre le plus voisin cladistiquement des *Gynandrotarsus* est *Pseudodichirus* qui est le moins évolué des deux groups. Ce dernier sous-genre est trouvé en Europe. Il est postulé que l'ancêtre des *Gynandrotarsus* traversa d'Europe à l'Amérique du nord à la fin du Crétacé ou au début du Tertiaire par une connection terrestre très large entre l'Europe et l'est de l'Amérique du nord. La distribution présente des espèces est étudiée et expliquée en relation aux anciens climats, et aux changements géologiques faunistiques et floristiques nord américains.

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## INTRODUCTION

My interest in the subtribe Anisodactylina began in 1967 when I revised the species of the genus *Dicheirus*, a member of Anisodactylina. In order to better understand the relationships of *Dicheirus* to other genera of Carabidae, I examined specimens of other groups of Anisodactylina and reviewed the literature on the subtribe. I found that the supra-specific classification of the subtribe was in great need of revision since workers had added and deleted genera until one could only state that the subtribe contained approximately 40 genera. I also found that the species of many genera and subgenera of Anisodactylina were in need of revision.

I have undertaken a comprehensive 5 part study of the Anisodactylina: (1) a reclassification of the supra-specific taxa of the subtribe on a world-wide basis; (2) revisions of the species of *Gynandrotarsus* and the North American species of *Notiobia*; (3) a revision of the species of the subgenus *Anadaptus*; (4) a revision of the Central and South American species of *Notiobia*; and (5) revisions of the species of the Australian and Oriental genera. The first and second parts are now presented. My revisions of *Gynandrotarsus* and North American *Notiobia* (including *Anisotarsus*) used with Lindroth's (1968) excellent treatment of the Harpalini of Canada and Alaska treat all North American species of Anisodactylina except a few species of the subgenus *Anadaptus*.

## MATERIALS

The taxonomic decisions in this paper are based on a comparison of characters found in adult specimens. Approximately 15,000 adult specimens were examined for the supra-

specific reclassification. An additional 10,533 specimens were examined for the revisions of the species of *Gynandrotarsus* and the North American species of *Notiobia*.

Types were examined during visits to the British Museum of Natural History, London, Great Britain; Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; Museum National d'Histoire Naturelle, Paris, France; and United States National Museum, Washington, D.C. Unless otherwise noted, I have seen the type of each species (and associated synonyms) of *Gynandrotarsus* and of the North American forms of *Notiobia*. In addition I have seen type or identified specimens of most of the species in other supra-specific taxa of Anisodactylina. The museums from which non type material was examined are listed in the acknowledgements section.

## METHODS

### Criteria for species, subunits of species and supra-specific taxa

For this study the following definition of a species given by Mayr (1969) is accepted: a species consists of "Groups of actually (or potentially) interbreeding natural populations which are reproductively isolated from other such groups". There is no direct information available on the presence or absence of interbreeding among forms in *Gynandrotarsus* and *Notiobia*. Also there is at most limited information on the ecology and biology of the various forms. Therefore the presence or absence of interbreeding must be inferred from an examination of color and of morphological characters. The underlying assumption of such an inference is that different species will be separated by a pronounced gap in color and/or morphological characters. I use the following criteria in delimiting species. Sympatric forms were considered to be separate species if they constantly differed in 1 or more color or morphological characters. Allopatric forms were considered as separate species if they differed in 1 or more color or morphological characters, and if the differences in these character(s) were roughly comparable to those found between other closely related species which were sympatric. None of the forms examined in this study exhibited parapatry.

Subspecies are not formally named in this paper. Characters other than those of morphology and color should be available for the recognition of formal taxa below the species level. Also a formal subspecific name has legal nomenclatural status and once proposed can never be abolished. I have therefore chosen to refer to subunits of species as "morphs". This is an informal term and names given to morphs need not be retained by subsequent workers who may disagree with my findings.

Simpson (1961) and Whitehead (1972) pointed out that the inclusiveness of genus group taxa is somewhat arbitrary. Hennig (1966) and Brundin (1966) asserted that supra-specific taxa which demonstrate sister group relationships must be given equal formal rank. This requirement is overly simplistic, leads to excessive splitting, and requires the recognition of numerous supra-specific categories in addition to the formally established ones such as subgenus, genus, subtribe, and tribe. Ball and Erwin (1969), Erwin (1970), and Darlington (1970) have objected to this requirement. Mayr (1969) listed 5 criteria for delimiting and ranking supra-specific taxa: (1) distinctness (size of gap); (2) evolutionary role (uniqueness of adaptive zone); (3) degree of difference (that is evolutionary divergence); (4) size of taxon; and (5) equivalence of ranking in related taxa. I have endeavored to take account of these 5 criteria in delimiting and ranking supra-specific taxa.

I have for the most part recognized only monophyletic supra-specific taxa, that is taxa composed of all the descendants of an immediate common ancestor. However, consideration of the criteria provided by Mayr has led me to recognize several paraphyletic groups. For example, the genus *Geopinus* which most likely evolved from the same common ances-

tor as several subgenera of the genus *Anisodactylus* is accorded separate generic status because of the large amount of evolutionary divergence and because of the ecological specialization of the single included species.

### Procedural methods

#### *Sorting of specimens employed in revisions of species.*

Sorting of specimens was done according to a systematic procedure to facilitate application of the criteria explained above for species and "morphs". Specimens were first grouped into series each composed of specimens with similar color and external morphology. The specimens of each series were next sorted according to geographical locality. The specimens of a series were then compared in regard to color and external morphology. If this comparison indicated the members of a series were probably conspecific, then the genitalia were examined from specimens distributed throughout the entire range of the "tentative" species. If such an examination supported the hypothesis of conspecificity, then the series was compared with other such series to determine if any of these series were conspecific. Specimens of an individual series, which on an examination of the genitalia seemed to be composed of smaller subunits, were sorted into these subunits. The subunits were then carefully compared to determine whether they warranted separate specific status. Any subunits which seemed to warrant separate specific status were compared with all other "tentative" species.

After a species was delimited, all specimens of it were further examined for intra- and interpopulational variation. For this examination, it was assumed that specimens of a species collected at the same exact locality were members of a single deme.

#### *Sorting of specimens employed in revisions of supra-specific groups.*

Specimens were first sorted according to named species of currently accepted supra-specific taxa. The species of each such supra-specific taxon were then examined to determine if they formed a single monophyletic group. Adjustments were made if the species of a given taxon appeared to represent 2 or more monophyletic groups, to represent only part of a single monophyletic group, or to represent elements of several different monophyletic groups.

During the grouping process, a tentative phylogeny was constructed and repeatedly modified until it seemed the most probable representation of the evolution of supra-specific taxa of Anisodactylina. The units of species or species groups were finally ranked into genera, subgenera and species groups on the basis of the criteria explained above.

### Dissecting techniques

Specimens in which the genitalia, hindwings, or mouthparts were to be removed were relaxed in boiling or nearly boiling distilled water for 2 to 5 minutes. Detergent such as "409 Household Cleaner" was usually added in order to simultaneously clean the beetle of any dust or grease. The specimen was next placed for 1 to 2 minutes in a beaker of distilled water to wash away any detergent residue. Watchmaker forceps with number 5 points were used for the dissections described below.

The genitalia could usually be removed through the genital opening. Forceps were inserted into the opening and moved from side to side to enlarge it. The genitalia were then grasped near their base and pulled out. This extraction procedure did not work on specimens which had been killed or preserved in formalin or alcohol solutions. In these specimens the abdomen was pulled off and the genitalia removed after cutting or tearing away the tergum.

The internal sac of the median lobe was then everted on several male specimens. The median lobe was first placed in boiling or nearly boiling 5 to 10 percent potassium hydroxide solution for 3 to 5 minutes to dissolve muscle tissue attached to the internal sac. Then

the median lobe was transferred to a small water-filled watch glass or a plastic lid from a prescription vial. A pair of forceps was used to clamp the basal bulb dorso-ventrally just distal to the basal orifice. These forceps were kept clamped in order to prevent fluid from escaping through this opening. A second pair of forceps was used to clamp the median lobe dorso-ventrally just distal to the first pair. The second pair was then moved distally and the median lobe again clamped. This procedure was continued until the ostium was reached. The fluid pressure resulting from repeating clamping often everted the sac.

In some specimens fluid pressure was not sufficient to evert the internal sac. A pair of forceps was then inserted through the ostium, and the internal sac was pulled out. This procedure was more likely to damage the internal sac and was used only when the above technique failed.

In some specimens it was impossible to evert the internal sac by any method. This apparently was due to the beetle having been killed or stored in formalin or a strong alcohol solution.

Female genitalia on which the valvifer, stylus, and proctiger were to be examined were usually placed in a small container of water under a stereoscopic microscope and muscles or membrane obstructing the field of view were removed with forceps. Sometimes the genitalia were first placed in hot potassium hydroxide solution for 1 to 5 minutes to facilitate this removal.

Female genitalia in which the spermatheca was to be examined were placed in boiling or nearly boiling potassium hydroxide solution for approximately 1 minute. They then were transferred to a small dish of water and examined under a stereoscopic microscope. If the spermatheca was still obscured by muscles and other tissue, this treatment was repeated as needed. Care had to be employed since excessive clearing would render the spermatheca nearly transparent.

Genitalia vials were used to store: median lobes with everted internal sacs; female genitalia with cleared spermathecae; mouthparts; hindwings; and various other small structures. These vials are plastic with soft plastic stoppers. They prove superior to glass vials with cork stoppers since glycerine will not leak from them. The body part was placed in the vial with forceps and several drops of glycerine added with a syringe. The vial was then stoppered, and the pin supporting the specimen run through the stopper.

Most median lobes with internal sacs not everted and female genitalia with spermathecae not cleared were glued with clear nail polish to a small card or point pinned immediately beneath the specimens. Some median lobes were pierced with a minuten pin attached to a piece of polyporous pith pinned beneath the specimen.

Hind wings and mouthparts were removed from the specimens by grasping their bases with forceps and pulling the structures off the insect. The hind wings and mouthparts were then usually treated as follows. Each of these structures was first placed in a container of 95 percent ethanol and then placed in clear nail polish which was applied to a small card pinned immediately beneath the insect. The hind wings were completely unfolded so that all areas were visible, and the mouthparts were arranged so that the desired part of them was visible for examination. This procedure minimized shrinking of membranous structures and provided a simple method of preserving wings and mouthparts for ready viewing without the necessity of preparing slides. It also had the advantage of directly associating each structure with the specimen from which it was removed.

## Measurements

*On specimens employed in species revisions.*

Total body length measurements were made for each species to give a general impression



of its size range. The 5 largest and 5 smallest specimens of each species were visually selected and measured as follows. The specimen being measured was placed sideways under a stereoscopic microscope with a calibrated ocular grid. The body length was measured along the side from the mandible apex to the abdominal apex. When the mandibles or abdomen of a specimen being measured were extended or retracted, the specimen was relaxed in hot water and the body parts arranged in normal position.

*On specimens employed in supra-specific revisions.*

Specimens were measured by the technique described above. However in many instances less than the 5 largest and 5 smallest specimens of each species were visually selected and measured.

## Illustrations

Line drawings of morphological characters were made with the aid of a drawing tube on a Wild stereoscopic microscope. Unless otherwise noted, the accompanying scale lines equal 1 mm. Distribution maps of taxa were made by using dots to represent localities.

Some readers may be interested only in the species revisions presented here, in the supra-specific revisions, or in the discussions on phylogeny and zoogeography. Therefore the illustrations are placed in the following order at the end of the text: (1) drawings of morphological characters and species distribution maps of assistance in identifying North American species of *Anisotarsus*, *Notiobia* (s. str.), and *Gynandrotarsus*; (2) drawings of morphological characters of assistance in identifying supra-specific taxa; and (3) diagrams and maps referred to in the discussions on phylogeny and zoogeography.

## Format

Each species or supra-specific description provides reference to: the original publication of the valid name of the taxon in the form in which this taxon was first published; and the original publication of each synonym in the form in which the synonym was first published. Many papers, especially regional checklists, are based on incorrectly identified material and therefore are of little value. Also the mere listing of references does not tell the reader what the reference said concerning the taxon. Such listing is better published in formal catalogues, such as the Csiki catalogue on Carabidae and the forthcoming revised carabid catalogues being prepared by T. L. Erwin, and is here omitted.

Taxonomically important papers are reviewed in full in a discussion section under the appropriate taxon. This discussion section also contains information concerning problems with types and reasons for synonymy or proposed taxonomic changes.

Lists of individual localities from which specimens were seen and of the museums loaning the specimens are omitted. The individual distributional maps provide a good impression of the range of each species. Readers desiring these data or other additional information may contact me.

Sections on distribution and material examined are included with each species description. Where sufficient information is available, sections on variation, flight, and bionomics are also included. The section on variation discusses intra- and interpopulational variation. The section on bionomics summarizes all available information on a species' phenology, ecology, biology and feeding habits. Much of the information concerning ecology was kindly supplied by G. E. Ball; this information is referred to as "Ball's data" in the various sections. The section on distribution and material examined outlines the general distribution of each species and gives the number of specimens examined. It also provides information on disjunct populations of a species.

The discussion section of each genus or subgenus whose species are not revised in this pa-

per provides a list of the included species. The author and date of original publication are provided for each such species, but in most instances the original description is not listed in the references cited section. Readers desiring such bibliographic information may consult standard catalogues such as Csiki (1932). An asterisk immediately behind the date of a species indicates that I have not examined specimens of that species. An asterisk behind a male or female symbol indicates that I have not examined specimens of that sex of the species in question.

### Abbreviations

The following abbreviations were used in the synonymy and discussion sections to identify museums containing type specimens:

BMNH	British Museum of Natural History, London, S.W. 7, Great Britain
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
MNHP	Museum National d'Histoire Naturelle, 45 bis rue de Buffon, Paris (V), France
UASM	University of Alberta, Strickland Museum, Edmonton, Alberta
USNM	United States National Museum Smithsonian Institution, Washington, D.C.

### Taxonomic Characters and Terminology

*Color.* — Body color is useful in distinguishing many taxa. Color is described with terms taken from Torre-Bueno (1962). Metallic tinges are frequently present on the dorsum and are often helpful in identification of taxa. Perception of such tinges is often affected by the type of light used, and the manner of illumination is therefore explained where appropriate.

*Microsculpture.* — Microsculpture is useful in characterizing some taxa. The primitive condition is that of an isodiametric mesh. Modifications encountered are: microsculpture reduced or absent; granulate; transversely stretched; consisting of fine transverse lines; and consisting of punctures. No matter what type of microsculpture is present, it is usually more prominent in female specimens. The microsculpture of some species appears composed of granulate mesh or of punctures depending on which angle light strikes the specimens. When the mesh is granulate, the flat areas between granulae appear as though punctured under certain lighting conditions.

*Head.* — The frontal fovea on each side of the head each bears a clypeo-ocular prolongation in some specimens. This prolongation (Fig. 46) appears as a groove or linear impression directed towards the general vicinity of the eye. When the fronto-clypeal suture joins the frontal fovea and ends there, the clypeo-ocular prolongation may appear to be a shallow continuation of this suture. The presence, absence, and degree of development of the clypeo-ocular prolongation are useful in distinguishing several taxa.

The presence, absence, and degree of development of a transverse suture between the mentum and submentum are useful in delimiting many taxa. In relatively plesiomorphic groups such as *Anisotarsus* the mentum and submentum are separated by a complete transverse suture which appears as a narrow transverse membranous band (Fig. 170). In most specimens of the genus *Progonochaetus* the suture is still visible medially but has disappeared laterally. In specimens of more apomorphic genera such as *Anisodactylus* the mentum and submentum have become completely fused and the former suture is at most indicated by a faint groove (Fig. 171). In dried specimens possessing a suture between the mentum and submentum, the suture may be shrunken and difficult to discern. Therefore the reader

should soak "doubtful" specimens in hot water for 2 to 3 minutes to make the suture more evident.

*Abdomen.* — The last visible sternum is referred to in descriptions as "sternum VI". This is the apparent sixth sternum and the morphological seventh sternum. The number of ambulatory setae on sternum VI of males is useful in separating some species. When only 1 pair is present, a single seta is placed on each side slightly laterad to the middle apex of the sternum. When 2 pairs are present, an additional seta is located on each side just lateral to the seta described above.

Most specimens of Anisodactylina have 1 pair of ambulatory setae on abdominal sterna III to V, 1 or 2 pairs on sternum VI, and patches of very short fine setae on sterna I and II under the trochanters and bases of the femora. When additional setae are present, they are referred to as "extra setae".

*Male genitalia.* — The median lobe of the male genitalia is frequently very important in separating species. The proximal enlarged bulb-like region which receives the basal orifice is referred to as the basal bulb. The portion between the basal bulb and the distal end of the dorsal membranous area is termed the shaft. And the portion between the distal end of the membranous dorsal area and the distal end of the median lobe is here called the apex. Frequently the apex is swollen distally producing a dorso-ventral thickening termed the apical disc. The parameres of males are fairly constant and do not offer readily apparent characters for defining taxa within the subtribe. The internal sac of the median lobe is useful in defining specific and supra-specific taxa in many groups of Carabidae. Within Anisodactylina, however the internal sac exhibits considerable intrapopulational variation and normally is of no assistance in delimiting species or even subunits of species.

*Female genitalia.* — The female genitalia provide useful characters for delimiting several supra-specific groups. There has been considerable disagreement among workers over homology and consequently also terminology of the structures of the female genitalia. Tanner (1927) studied the genitalia of female Coleoptera and concluded that: (1) the genitalia consist of the eighth, ninth and tenth abdominal segments and appendages; (2) the appendages of the eighth and tenth segments have disappeared; (3) the appendages of the ninth segment consist of the styli, coxites, and valvifers and are borne on the distal end of the ninth sternite; and (4) the proctiger forms part of the tenth tergite.

Lindroth and Palmen (1956) discussed the female genitalia of Coleoptera and Lindroth (1957) provided a table containing terms used by previous workers. Lindroth and Palmen (1956) concluded that the ninth sternum of female Coleoptera "as a rule is divided into a pair of "hemisternites" . . . between which the vulva . . . is situated. Each hemisternite usually bears an articulating process, the stylus . . .". The term "hemisternite" as used by Lindroth and Palmen (1956) refers to the same plate-like structure as does the "valvifer" of Tanner (1927). The basal segment of the structure termed the "stylus" by Lindroth and Palmen (1956) refers to the "coxite" of Tanner (1927). (Lindroth, 1957, mistakenly listed the term "coxites" of Tanner (1927) as being equivalent to the term "hemisternite".) The apical segment of the "stylus" of Lindroth and Palmen (1956) is equivalent of the "stylus" of Tanner (1927).

John Kingsolver kindly made available to me unpublished notes and drawings of R. E. Snodgrass which are stored at the Smithsonian Institution, Washington D. C. The notes and drawings refer to a dissection by Snodgrass of a species of the carabid genus *Pterostichus* (species not stated). These notes are quoted in part below to make them available to other workers and to hopefully assist in stabilizing the terminology of parts of the female genitalia. The drawings of Snodgrass are shown in Figs. 167, 168, 169.

"The normally exposed part of the abdomen ends with the seventh segment. From this

the eighth segment consisting of a narrower tergal and sternal plate is protractile. Beyond the eighth seg [sic] is a wide annulus of membrane (called IX seg. by Tanner), and beyond this the ninth segment bearing the pair of ventrolateral appendages. The tenth segment, a proctiger, is small and mostly concealed within the ninth seg.

"The two-segmented genital appendages are supported on each side by a prominent oval plate (a), the anterior end of which is broadly invaginated and of an apodemal nature. These plates Tanner calls the "valvifers". The proximal segment of the free part of the appendage (b) (the "coxite" of Tanner) is elongate, at the terminal segment (c) ("stylus" of Tanner) is a hook-like claw curved inward and outward.

"The genital appendage as a whole has little resemblance to an ordinary gonopod of an ovipositor. The supporting plate, however, has two muscles arising on the ninth tergum: one (1) a large oblique muscle, the other (2) a flat muscle with . . . fibers from edge of T to edge of plate a. The basal seg. of the appendage has a muscle (3) from . . . ventral surface of plate a to its proximal ventral extremity. The hook has two muscles, a large flat fan of fibers (4) arising on inner face of plate a, inserted on dorsal angle of its base, and a small muscle (5) arising proximally on b and having same insertion as 4. Evident that a belongs to IX seg. and that it may be the valvifer of this seg., but musculature of b and c have little resemblance to valvifer muscles of gonopophyses; though b + c may represent a two-segmented stylus. Since the valvifer is the "coxite", Tanners (sic) distinction between valvifer and "coxite" is not logical. If b, b are bases of appendages, then a, a do not represent the sternum of IX seg. (as supported by Tanner), since the latter would lie between the appendages."

These notes of Snodgrass suggest that the 2 segmented structure ("b + c" of Fig. 167) is best termed the "stylus". And since the plate-like structure supporting the stylus ("a" of Fig. 167) may represent the valvifer, it seems best to term it "valvifer" rather than accept the additional term "hemisternite" proposed by Lindroth and Palmen (1956).

## SYSTEMATICS

### The Subtribe Anisodactylina

Anisodactylides Lacordaire, 1854: 257, 268

Anisodactylites Jacquelin du Val, 1857: 35, 64

Anisodactyli G. Horn, 1881: 176, 184

Anisodactylinae H. W. Bates, 1882: 49

Anisodactylidae Peringuey, 1896: 417

Anisodactylini Tschitscherine, 1900: 344, 351, 367

Anisodactylina Jakobson, 1907: 370

Anisodactylitae Jeannel, 1942: 600

*Diagnosis.* — Head with 1 seta over each eye. Mandible lacking seta in scrobe. Antenna inserted on side of head directly between eye and base of mandible; segments III to XI or IV to XI covered with setae or pubescence; segments I to II or I to III with rings of setae at apex only. Mentum (except in *Rhysopus*) with 1 seta on each side of median area. Ligula with 2 distal ventral setae and lacking additional setae except in *Scybalicus*, *Pseudanisotarsus*, and *Progonochaetus*. Labial palp with penultimate segment plurisetose on anterior margin; terminal segment subequal in size to penultimate segment, not minute. Forecoxal cavity closed and uniperforate. Midcoxal cavity entirely enclosed by sterna, mesepimeron not reaching midcoxal cavity. Foretibia with inner spur terminal, outer spur subapical; both spurs more or less associated with antennal cleaner. Foretarsus of ♂ (except in some *Progonochaetus* (*Eudichirus*) *jeanneli* [R. Clarke, personal communication] and in some *Dicheirus dilatatus angulatus*) with segments I to IV or II to IV laterally expanded and

spongy pubescent beneath. Midtarsus of ♂ also modified in most species. Scutellum of mesothorax normally exposed. Elytron with basal bead extending to or just short of scutellum; lacking epipleural plica at apex. Abdomen normally with 6 visible sterna. Median lobe when symmetrical with distal portion of shaft containing ostium not deflected to the left; basal bulb well developed; in most species shaft immediately distal to basal bulb bent and giving arcuate shape to median lobe. Parameres short and broad, conchoid, or oviform; similar in shape except right one always smaller; lacking setae.

*Description.* Body length 6.3 to 19 mm. Body form various.

*Color.* Body generally rufopiceous to black, with brighter colors or metallic tinges in some taxa.

*Head.* Labral apex straight to strongly emarginate medially. Clypeus with apex straight to prominently emarginate medially, with 1 long seta at each outer distal angle unless otherwise stated. Eye small to large. Frons with varied fovea; microsculpture usually of isodiametric mesh. Mentum with or without tooth situated medially on distal margin of mentum; except for *Rhysoptus* (which lacks setae) with 1 seta on each side of median area of apex, when tooth present such seta situated at lateral base of tooth. Mentum and submentum separated by a complete transverse suture (Fig. 170) or fused laterally but still separated medially; or completely fused (Fig. 171). Submentum of all taxa except *Phanagnathus overlaeti* with 1 long inner and 1 short outer seta on each side, in *Phanagnathus overlaeti* with 1 long seta on each side. Ligula with 2 distal ventral setae and lacking additional setae except in *Pseudanisotarsus*, *Progonochaetus*, and *Scybalicus hirtus*. Paraglossa membranous and glabrous unless otherwise stated. Penultimate segment of labial palp plurisetose on anterior margin.

*Thorax.* Pronotum of various shapes; 1 long seta on lateral margin near mid point except 2 lateral setae on each side in *Progonochaetus* and *Diachromus*; apical bead present at least laterally except in *Dicheirus*; microsculpture various, but of isodiametric mesh in most specimens. Apex of prosternal lobe with several prominent setae.

*Legs.* Foretarsus of all ♂♂ and midtarsus of most ♂♂ with segments I to IV or II to IV laterally expanded and with ventral spongy pubescent vestiture except in some ♂♂ of *Progonochaetus* (*Eudichirus*) *jeanneli* [R. Clarke, personal communication] and of *Dicheirus* *dilatatus angulatus*.

*Elytron.* Humerus with or without tooth; scutellar stria unless otherwise noted short and arising from near base of stria II and with ocellate puncture near its base; intervals flat to convex, with or without setigerous and non-setigerous punctures; subapical situation various; microsculpture various but of isodiametric mesh in most specimens.

*Hind wing.* Full in most species but vestigial or varied from full to vestigial in some species.

*Abdomen.* Sterna III to V each with 1 pair of ambulatory setae, with extra setae in some taxa; sternum VI of ♀ with 2 pairs of ambulatory setae, except genus *Allocinopus* with only 1 pair such setae; sternum VI of ♂ with 1 or 2 pairs of ambulatory setae.

*Male genitalia.* Median lobe arcuate and symmetrical in most species (except arcuate and asymmetrical in *Notiobia tucumana* and *Xestonotus lugubris*, twisted distally in *Dicheirus piceus*, and *Anisodactylus binotatus*, only slightly arcuate in species of the subgenus *Pseudohexatrachus*); membranous area of dorsum various; apical disc present or absent; venter sclerotized, except membranous in 1 species of genus *Allocinopus*. Parameres short and broad, conchoid or oviform, right similar to left but smaller.

*Female genitalia.* Valvifer various in shape, degree of sclerotization, and distal pubescence. Stylus with 2 segments, segments fused in *Pseudanisodactylus*; unless otherwise noted basal segment lacking setae and distal segment with 2 distal setae on mesal margin and with lateral

margin excavate (Fig. 237). Proctiger in most species consisting of irregular semi-sclerotized area with stout setae on each side of anus. Spermatheca (Fig. 128) tubular with distal portion annulated (distal annulated portion shorter in some species than shown in Fig. 128).

Internal organs. Rectum with 2 rows of oval rectal glands, 3 glands in each row.

## Discussion

Anisodactylina like other subtribes of Harpalini has been differently defined by various authors, primarily because those authors studied only those Anisodactylines from specific regions of the world. Rather than spend needless pages detailing past misconceptions concerning the subtribe, I shall concentrate on discussing the subtribe as defined in this paper.

The subtribe Anisodactylina is here defined to include all those Harpaline genera which agree with the diagnosis given earlier. Twenty four genera of Harpalines clearly fit this diagnosis and are regarded as members of the subtribe Anisodactylina. The genus *Smirnovia* Lutshnik, 1922 was described by Lutshnik (1922) for the single species *tristis* Lutshnik, 1922 from Turkestan. Lutshnik (1922) declared *Smirnovia* to be closely related to the genus *Anisodactylus* because of the similar general habitus of *Smirnovia tristis* and *Anisodactylus* (*A.*) *binotatus*. Schauburger (1926) listed *Smirnovia* as a member of Anisodactylina, and subsequent workers have accepted this placement. I have not been able to examine specimens of *Smirnovia tristis*, but I have read the original description of this taxon. According to the original description, *Smirnovia tristis* has 2 supra-orbital setae over each eye; all other members of the tribe Harpalini have only a single such seta over each eye. Probably the genus *Smirnovia* belongs in a different tribe. Until specimens of *Smirnovia* can be examined, the genus is best treated as *incertae sedis* within the tribe Harpalini.

Basilewsky (1950) included *Anisochirus* Jeannel, 1946 as a valid genus belonging to Anisodactylina. This genus was described by Jeannel (1946) as monotypic, containing only the species *alluaudi* based on a single male from Madagascar. Basilewsky (1950) noted that *Anisochirus alluaudi* differed from all other African and Madagascar Anisodactylines by having the distal portion of the median lobe containing the ostium deflected to the left as in species of *Harpalus*. Quite possibly Basilewsky was not able to examine the holotype of *Anisochirus alluaudi* since his descriptions of the genus and species are quite short, and his drawing of the median lobe of *alluaudi* looks like a redrawing of that provided by Jeannel (1948).

George E. Ball kindly examined the holotype of *alluaudi* at the MNHP and supplied the following information. The median lobe indeed did have the distal portion containing the ostium deflected to the left. The holotype was glued to a card which made examination of the tarsal vestiture difficult. Removal of the holotype from the card revealed that the tarsal vestiture was biseriate as in *Harpalus*. And the holotype keyed out in Basilewsky (1950, 1951) to *Harpalus madagascariensis* Dejean, 1831 which was cited by Basilewsky (1951) as being common throughout Madagascar. Comparison with identified specimens of *madagascariensis* indicated that *alluaudi* is a junior synonym of that species (NEW SYNONYMY), and thus that *Anisochirus* is congeneric with *Harpalus* (NEW SYNONYMY).

The monotypic genus *Xenophonius* G. Müller, 1942 was treated as a member of Anisodactylina by Basilewsky (1950) who apparently saw only female specimens of *X. hirtus* G. Müller, 1942. I have examined the male holotype of *X. hirtus* and found that: the foretarsus has the apex of segment I and all of segments II to IV moderately expanded laterally and biseriate beneath; the elytron is iridescent; and the ostium of the median lobe is dorsal in position. Because of this combination of characters, *X. hirtus* and the genus *Xenophonius* are not members of the subtribe Anisodactylina and are here transferred to the Selenophori group of the subtribe Harpalina.

I believe that the 24 genera examined by me and treated as members of Anisodactylina constitute a monophyletic group. However it is not possible to state that the subtribe is defined on the basis of clearly apomorphic character states. The main features defining the subtribe are: penultimate segment of labial palp plurisetose on anterior margin; ventral vestiture of male fore- and midtarsi spongy pubescent; median lobe with distal portion of shaft containing ostium not deflected to the left. The unmodified form of median lobe would seem to be a plesiomorphic feature within the tribe Harpalini. Spongy pubescent tarsal vestiture is restricted to Anisodactylina and the sub-tribe Pelmatellina and is probably apomorphic. The plurisetose condition of the penultimate segment of the labial palp may or may not be apomorphic.

If spongy pubescent tarsal vestiture is indeed apomorphic, then the subtribe Pelmatellina is the sister group of Anisodactylina. Species of Pelmatellina possess the spongy pubescent tarsal vestiture found in Anisodactylina but differ from species of that subtribe by having 2 or 3 setae on the anterior margin of the penultimate segment of the labial palp. In addition, species of at least the Pelmatelline genera *Nemaglossa*, *Pelmatellus*, and *Thenarellus* differ from species of Anisodactylina by lacking setae at the apex of the prosternal lobe (personal communication from H. Goulet who is revising supra-specific taxa of Pelmatellina —other 2 genera of that subtribe not yet examined for presence or absence of setae).

Further elucidation of the plesiomorphy and apomorphy of the characters defining Anisodactylina will have to wait until the other 6 subtribes of Harpalini have been revised on a world-wide basis.

### Key to the Genera and Subgenera of the Subtribe Anisodactylina

#### *Notes concerning the key*

The 37 supra-specific taxa of which I have seen specimens are separated in the key below. The number of pronotal lateral setae is used as a separating character in the first couplet. The pronotal lateral setae are more elongate than any other pronotal pubescence and therefore easily discerned even on densely pubescent specimens. When the pronotal lateral setae are broken off, their number can still be determined by careful examination since each such seta arises from a socket slightly larger than that associated with other pronotal pubescence.

#### *Key to the Genera and Subgenera of the Subtribe Anisodactylina*

- |       |   |  |
|-------|---|--|
| 1     | Pronotum with 2 lateral setae on each side (in most specimens anterior seta located before or in midregion of lateral margin and posterior seta located in region of posterior angle) . . . . . | 2  |
| —     | Pronotum with 1 lateral seta on each side (such seta situated in midregion of lateral margin) . . . . .   | 4  |
| 2 (1) | Dorsum tricolored, head and base of elytron rufotestaceous, pronotum black, apex of elytron violaceous or bluish brown; range England, Europe, Mediterranean area . . . . .                     | <i>Diachromus</i> Erichson, p. 381           |
| —     | Dorsum not so colored, rufopiceous to black; range Madagascar and Africa south of the Sahara Desert . . . . .   | 3  |
| 3 (2) | Pronotum (Fig. 187) with side sinuate before acute, outward projected posterior angle . . . . .   | <i>P. (Eudichirus)</i> Jeannel, p. 343       |
| —     | Pronotum (Figs. 184, 186) with side not sinuate and posterior angle not acute and outward projected . . . . .   | <i>P. (Progonochaetus)</i> G. Müller, p. 342 |
| 4 (1) | Mentum and submentum separated by complete transverse suture (Fig. 170) . . . . .   | 5  |
| —     | Mentum and submentum completely fused (Fig. 171) . . . . .  | 18   |
| 5 (4) | Body (except part of elytron in some specimens) with dense pubescence . . .   | 6  |

- Body without dense pubescence ..... 7
- 6 (5) Pronotum suborbiculate (Fig. 181); clypeal apex raised into bead; range Africa to India ..... *Crasodactylus* Guérin-Meneville, p. 286
- Pronotum semi-cordate (Fig. 183); clypeal apex not raised into bead; range England, Europe, Mediterranean area ..... *Scybalicus* Schaum, p. 339
- 7 (5) Pronotum (Fig. 180) suborbiculate; AND lateral depression prominently flattened and sharply delimited from convex disc by discrete groove; AND apex of ligula not expanded laterally; AND abdominal sternum VI of ♀ with distal margin enlarged medially as plate-like area in posterior view (Fig. 205); range Australia ..... *Cenogmus* Sloane, p. 287
- Pronotum various in shape; pronotal lateral depression various, if sharply delimited from convex disc then apex of ligula broadly expanded laterally and pronotum cordate; abdominal sternum VI of ♀ unmodified ..... 8
- 8 (7) Pronotal disc pubescent at least along lateral part of apex; abdominal sterna with extra setae; range temperate southern South America ..... 9
- Pronotal disc glabrous except for single lateral seta on each side; extra setae on abdominal sterna present or absent; range New World, and Australian Region ..... 10
- 9 (8) Ligula with apex narrow, not laterally expanded, and with dorsum bearing 4 to 5 distal setae; pronotum not strongly cordate, lateral depression not sharply delimited; pronotal pubescence extended along lateral portions of basal and apical margins and along side; elytral intervals I, III, V, and VIII each with row of dorsal setigerous punctures ..... *Pseudanisotarsus* new genus, p. 290
- Ligula with apex strongly expanded laterally and dorsum lacking setae; pronotum strongly cordate and with lateral depression broadly concave and sharply delimited from disc; pubescence on pronotum restricted to lateral part of apex; odd and in some specimens also even elytral intervals each with irregular row of non-setigerous punctures ..... *Criniventer* van Emden, p. 292
- 10 (8) Body depigmented, testaceous in color; body length 9.5 mm or less; range New Zealand ..... *Triplosarus* H. W. Bates, p. 285
- Body not depigmented, rufopiceous to black or metallic in color; body length often more than 9.5 mm; range Australian Region (including New Zealand), New World, Africa ..... 11
- 11 (10) Third and often other elytral intervals with 3 or more dorsal setigerous punctures (such punctures frequently extended to basal area of elytron) ..... 12
- Third elytral interval with 1 or 2, dorsal setigerous punctures ..... 13
- 12 (11) Frontal fovea of head lacking clypeo-ocular prolongation; median lobe lacking apical disc; range Australian Region and eastern part of Oriental Region ..... *Gnathaphanus* MacLeay, p. 289
- Frontal fovea of head with clypeo-ocular prolongation (may be faint); median lobe with button-like apical disc (Figs. 210, 211); range Ethiopian Region ..... *N. (Diatypus)* Murray, p. 337
- 13 (11) Pronotum cordate and with side sinuate before posterior angle; AND gena wide, narrowest part of gena between mouth and eye as wide or wider than maximum width of first antennal segment; AND dorsum without metallic tinges; abdominal sternum VI of ♂ with 1 pair of ambulatory setae; range New Zealand ..... *Allocinopus* Broun, p. 284
- Pronotum not cordate and side not sinuate before posterior angle; OR if pronotum cordate and side sinuate then gena narrow with narrowest part between



- mouth and eye much narrower than maximum width of first antennal segment; OR dorsum with metallic tinges, abdominal sternum VI of ♂ with 2 pairs of ambulatory setae; range Australian Region (including New Zealand) and New World ..... 14
- 14 (13) Abdominal sterna with extra setae (such setae may be very short and fine); AND mental tooth present; AND hindtarsus stout with first segment approximately twice as long as wide and always shorter than II + III; range Australian Region and as far towards Eurasia as Sumatra and Java ..... *Hypharpax* MacLeay, p. 388
- Abdominal sterna lacking extra setae; OR mental tooth absent; hindtarsus of most specimens not stout; range Australian Region, and New World ..... 15
- 15 (14) Gena narrow, at narrowest point narrower than maximum width of first antennal segment; OR frontal fovea of head with clypeo-ocular prolongation; eye of most specimens large and protruding ..... 16
- Gena wide, at narrowest point wider than maximum width of first antennal segment; frontal fovea of head lacking clypeo-ocular prolongation; eye of most specimens not large and protruding; range New World and Australian Region ..... *N. (Anisotarsus)* Chaudoir, p. 295
- 16 (15) Frontal fovea of head with clypeo-ocular prolongation; range tropical and subtropical areas of the New World ..... *N. (Notiobia)* Perty, p. 321
- Frontal fovea of head lacking clypeo-ocular prolongation ..... 17
- 17 (16) Frontal fovea of head large, prominent; supra-antennal ridges strongly divergent anteriorly from eyes; eye large and protruding; range tropical and subtropical areas of the New World ..... *N. (Notiobia)* Perty, p. 321
- Frontal fovea of head small, not prominent; supra-antennal ridges various, in most specimens not strongly divergent anteriorly from eyes; size of eye various; range temperate areas of the New World but extending along mountains into tropical and subtropical areas and also present in the Australian Region ..... *N. (Anisotarsus)* Chaudoir, p. 295
- 18 (4) Foretibia (Fig. 195) with apical portion strongly expanded laterally and with large excavate dilation at external apex; head with preocular sulcus receiving first antennal segment when in repose; range eastern North America ..... *Geopinus* LeConte, p. 377
- Foretibia with apical portion not strongly expanded laterally and without large excavate dilation at external apex; head lacking preocular sulcus ..... 19
- 19 (18) Dorsum, including all of elytron, densely pubescent ..... 20
- Dorsum mainly glabrous, elytron at most pubescent along margins ..... 24
- 20 (19) Dorsum tricolored with head and pronotum black; base of elytron rufotestaceous; apex of elytron violaceous brown; AND foretibial apical spur trifid (Fig. 45); range Europe, Mediterranean area, Syria, Transcaspien ..... *Gynandromorphus* Dejean, p. 380
- Combination of morphological characters not as above ..... 21
- 21 (20) Pronotal apical bead absent; foretibial apical spur trifid (Fig. 45); range western North America ..... *Dicheirus* Mannerheim, p. 381
- Pronotal apical bead present at least laterally; foretibial spur lanceolate (Fig. 188) or angulately swollen at sides (Fig. 189) ..... 22
- 22 (21) Ligula apex not expanded laterally (Fig. 178); dorsum with head and pronotum testaceous to rufotestaceous, elytron piceous and strongly iridescent due to microsculpture of extremely fine dense lines; range eastern North America

- ..... *A. (Amphasia)* Newman, p. 380
- Ligula apex expanded laterally (Fig. 177); dorsum not colored as above; elytron of some specimens with metallic tinges but microsculpture always of isodiametric mesh ..... 23
- 23 (22) Dorsum dull black, lacking metallic tinges; AND pronotum with side evenly rounded from apex to base and basal impression shallow and not separated from lateral margin by a convexity; range eastern North America ..... *A. (Pseudamphasia)* Casey, p. 379
- Dorsum with metallic tinges OR partly testaceous to rufotestaceous; OR pronotum with side sinuate before posterior angle OR with prominent linear basal impression separated from lateral margin by a convexity ..... *A. (Anadaptus)* Casey, p. 373
- 24 (19) Pronotum with lateral depression abruptly set off from convex disc by prominent inflexion of integument in apical 4/5 (frontispiece); elytral stria sharp, semi-rectangular in section; dorsum with metallic green or aeneous tinge; range eastern United States ..... *A. (Pseudaplocentrus)* new subgenus, p. 377
- Pronotum lacking such inflexion of integument; elytral stria rounded in section, not extremely sharp; dorsum with or without metallic tinge ..... 25
- 25 (24) Dorsum bicolored, head and base of elytron rufotestaceous, pronotum and median and apical portions of elytron bluish black; range Europe, Mediterranean area ..... *A. (Pseudhexatrichus)* new subgenus, p. 352
- Dorsum not colored as above ..... 26
- 26 (25) Frontoclypeal suture extremely deep, obliterating frontal fovea and continuing postero-laterally towards eye as very deep clypeo-ocular prolongation; AND mentum lacking tooth and setae; range Java, Sumatra, Indochina ..... *Rhyssopus* Andrewes, p. 347
- Frontoclypeal suture not extremely deep; AND mentum with or without median mental tooth, bearing 1 seta on each side of median area ..... 27
- 27 (26) Pronotum with broadly rounded posterior angle; AND dorsum covered with fine nonsetigerous punctures; AND microsculpture obsolescent or absent dorsally; range Sumatra, Philippines, Indochina, Japan ..... *Harpalomimetes* Schauburger, p. 346
- Combination of morphological characters not as above ..... 28
- 28 (27) Ligula narrow with apex not expanded (Fig. 175) ..... 29
- Ligula broader with apex expanded laterally (Figs. 176, 179) ..... 32
- 29 (28) Third elytral interval with 3 to 6 setigerous punctures in row from apex to or nearly to base; AND mentum with median tooth; range temperate southern South America ..... *Anisostichus* van Emden, p. 338
- Third elytral interval with at most 2 setigerous punctures, not with row from apex to base; OR mentum lacking median tooth ..... 30
- 30 (29) Mentum with prominent long median tooth (Fig. 172); range Oriental Region, Tibet, China, Japan, and extending as far towards Australia as New Guinea ..... *Chydaeus* Chaudoir, p. 345
- Mentum lacking tooth ..... 31
- 31 (30) Frontal fovea of head bearing prominent clypeo-ocular prolongation; segments II to IV of hindtarsus of both sexes and segments II to IV of fore- and mid-tarsus of ♀ with dense ventrolateral cover of somewhat thickened setae; median lobe of ♂ symmetrical; range Madagascar and Oriental Region ..... *Pseudognathaphanus* Schauburger, p. 344

- Frontal fovea of head lacking clypeo-ocular prolongation; tarsi lacking dense ventro-lateral cover of somewhat thickened setae; median lobe of  $\delta$  asymmetrical (Figs. 212, 213); range eastern North America ..... *Xestonotus* LeConte, p. 347
- 32 (28) Mentum with prominent long median tooth (Fig. 172); dorsum of mandible not striate; range Oriental Region, Tibet, China, Japan, extending as far towards Australia as New Guinea ..... *Chydaeus* Chaudoir, p. 345
- Mentum lacking tooth or if tooth present then not prominent; AND/OR dorsal apex of mandible striate ..... 33
- 33 (32) Foretibial apical spur lanceolate (Fig. 188), swollen laterally (Fig. 189), or in a few specimens of *Anadaptus* subtrifid (190), not trifid ..... 38
- Foretibial apical spur trifid (Fig. 45) ..... 34
- 34 (33) Clypeus with 1 seta at each outer distal angle ..... 35
- Clypeus with 2 or more setae at each outer distal angle ..... 37
- 35 (34) Pronotal lateral base including basal fovea covered with small dense non-setigerous punctures; elytron of some specimens also covered with small dense non-setigerous punctures; valvifer of  $\varphi$  triangular and with distal setae (Fig. 218); range Korea, Japan, China, India, Burma, Indochina ..... *A. (Anisodactylus)* Dejean, p. 349
- Pronotal lateral base not covered with small dense non-setigerous punctures (basal fovea may however have a few scattered small non-setigerous punctures; elytron not covered with small dense non-setigerous punctures; valvifer of  $\varphi$  subtriangular and lacking distal setae (Figs. 130, 220) ..... 36
- 36 (35) Hindtarsus with segment I as long as or longer than II + III; valvifer of  $\varphi$  with concave area along distal margin (Fig. 130); range North America ..... *A. (Gynandrotarsus)* LaFerté, p. 354
- Hindtarsus with segment I shorter than II + III; valvifer of  $\varphi$  lacking concave area along distal margin (Fig. 220); range Mediterranean area ..... *A. (Pseudodichirus)* Lutshnik, p. 354
- 37 (34) Foretibia of  $\delta$  with inner proximal basal margin strongly and abruptly emarginate (Fig. 192); dorsum of many specimens with metallic tinge; valvifer of  $\varphi$  subtriangular and with truncate apex (Fig. 222); range England, Europe to Norway and southern Russia, Balkan Peninsula, and Mediterranean area ..... *A. (Hexatrichus)* Tschitscherine, p. 353
- Foretibia of  $\delta$  with inner proximal basal margin not strongly and abruptly emarginate (Figs. 193, 194); dorsum without metallic tinge; valvifer of  $\varphi$  triangular (Figs. 217, 218); range eastern North America ..... *A. (Anisodactylus)* Dejean, p. 349
- 38 (33) Body with short semicordate pronotum and long parallel sided elytra; AND mandible prolonged with striate dorsal surface; AND labral apex strongly emarginate medially; range eastern North America ..... *A. (Spongopus)* LeConte, p. 374
- Combination of morphological characters not as above ..... 39
- 39 (38) Body broad and *Amara*-like and with metallic greenish, aeneous, bronze, or bluish tinges on dorsum ..... *A. (Aplocentrus)* LeConte, p. 375
- Body not broad and *Amara*-like and lacking dorsal metallic tinges ..... 40
- 40 (39) Hindtarsus stout with segment I shorter than II + III ..... 41
- Hindtarsus not stout and with segment I equal to or longer than II + III .... 42
- 41 (40) Body of most specimens narrow and subcylindrical; outer distal angle of clypeus

- of many specimens with 2 or more setae; dorsum of many specimens with rufotestaceous or metallic tinged areas; median lobe of ♂ with button-like apical disc (Figs. 206, 207); valvifer of ♀ various but never triangular in form, with or without distal setae; range North America . . . . . *A. (Anadaptus)* Casey, p. 373
- Body not narrow and subcylindrical; outer distal angle of clypeus with 1 seta; dorsum piceous to black, never with rufotestaceous or metallic tinged areas; median lobe of ♂ lacking apical disc; valvifer of ♀ triangular (Figs. 217, 218) or lobed (Fig. 221) in form and with distal setae . . . . . 42
- 42 (40, 41) Entire dorsum densely covered with small nonsetigerous punctures; valvifer of ♀ with distal setae, triangular or lobed in shape; (Figs. 217, 218, 221); range Eurasia and North America . . . . . 43
- Entire dorsum not densely covered with small non-setigerous punctures; valvifer of ♀ with distal setae and triangular in shape (Figs. 217, 218); range North America and Eurasia excluding Japan, Korea and tropical Asia . . . . . *A. (Anisodactylus)* Dejean, p. 349
- 43 (43, 42) Third elytral interval bearing dorsal setigerous puncture near middle or apical 1/3 (puncture and setae on some specimens small and difficult to discern at magnifications less than 50x); valvifer of ♀ triangular in shape (Figs. 217, 218,); range North America and Eurasia excluding Japan, Korea and tropical Asia . . . . . *A. (Anisodactylus)* Dejean, p. 349
- Third elytral interval lacking dorsal setigerous puncture; valvifer of ♀ lobed in shape (Fig. 221); range Japan, Korea and China . . . . . *A. (Pseudanisodactylus)* new subgenus, p. 351

### 1 genus *Allocinopus* Broun

*Allocinopus* Broun, 1903: 607. [TYPE SPECIES: *Allocinopus sculpticollis* Broun, 1903, by monotypy].

*Description.* — Body length 6.3 to 11.3 mm. Body relatively elongate.

Color. Body rufopiceous to black, no metallic tinge on dorsum.

Head. Labral apex slightly to moderately emarginate medially. Clypeus with apex straight to prominently emarginate, when prominently emarginate exposing base of labrum in many specimens. Eye normal to very small. Frons with fovea punctiform; microsculpture of isodiametric mesh, obsolescent medially in some specimens. Mentum with prominent tooth. Mentum and submentum separated by complete transverse suture. Ligula narrow, not expanded at apex. Paraglossa, slightly longer than ligula.

Thorax. Pronotum cordate; lateral and basal beads complete; apical bead present laterally; microsculpture of isodiametric mesh or obsolete. Metepisternum wider than long.

Legs. Foretibia with distal portion slightly expanded laterally; apical spur lanceolate or slightly swollen basally. Hindfemur with 2 long setae on posterior margin. Hindtarsus with segment I shorter than II + III. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with apex of segment I in most specimens and all of segments II to IV in all specimens laterally expanded and spongy pubescent beneath.

Elytron. Humerus with or without small tooth; scutellar stria arising from base of stria II, with or without ocellate puncture at base, short or elongate and joined distally to distal portion of stria I, or in some specimens elongate and capturing distal portion of stria I and with basal portion of stria I short and appearing to be the scutellar stria; intervals flat to very slightly convex; interval III with or without dorsal setigerous puncture on apical 1/3 or 1/4;

microsculpture of isodiametric mesh, transverse mesh, or obsolete.

Hind wing. Vestigial.

Abdomen. Sterna III to V with extra setae in some ♂♂; sternum VI with 1 pair of ambulatory setae in both sexes.

Male genitalia. Median lobe with membranous area of dorsum short, not reaching basal bulb; apical disc absent; venter of shaft membranous in species labeled as *latitarsis*, sclerotized in other species.

Female genitalia. In *castaneus* and *angustulus* valvifer stylus, and proctiger absent and ovipositor consisting of membranous extension of vagina. In *sculpticollis* valvifer moderately sclerotized, not vestigial or absent, with 1 or 2 distal setae; stylus unmodified except basal segment with 2 seta at distal lateral margin; proctiger unmodified. Spermatheca unmodified in all species in which females were examined.

*Discussion.* — Csiki (1932) listed 5 species in this endemic New Zealand genus: *angustulus* Broun, 1912; *castaneus* Broun, 1912; *ocularis* Broun, 1908; *sculpticollis* Broun, 1903; *smithi* Broun, 1912. I have not examined specimens of *ocularis* or *smithi*. The BMNH contains a series of male specimens labeled as "*Allocinopus latitarsis*". I have not located a published description of an *Allocinopus latitarsis* nor have I found a species, in another genus, which might have provided the specific name for these specimens. The specimens labeled as *latitarsis* seem to agree well with the original description of *smithi* and may be members of that species. The species of *Allocinopus* are in need of revision.

The species in this genus exhibit variation in 3 characters normally stable enough to be used in defining genera and to a lesser degree subgenera. The external female genitalia (valvifer, stylus, and proctiger) are absent in *castaneus* and *angustulus* (or at least not visible at 120 magnification) and present in *sculpticollis* (females of other species not seen). The median lobe of a species labeled as *latitarsis* (see above) has the venter membranous between the basal bulb and apex while the median lobe of other examined species has the venter completely sclerotized. Lastly, many males of *sculpticollis* have extra setae on abdominal sterna III to V.

Despite these differences the genus appears to be a discrete monophyletic unit defined by the following character combination (\*indicates character clearly apomorphic) eye small or almost vestigial\*; mentum with prominent tooth and separated from submentum by complete transverse suture; ligula narrow; metepisternum wider than long; sternum VI of female with only 1 pair of ambulatory setae (Sternum VI has 2 pairs in females of all other genera in subtribe)\*; and median lobe with membranous area of dorsum short and not extended to basal bulb.

## 2 genus *Triplosarus* H. W. Bates

*Triplosarus* H. W. Bates, 1874: 270. [TYPE SPECIES: *Triplosarus fulvescens* H. W. Bates, 1874, by monotypy].

*Description.* — Body length approximately 9 mm. Body rather stout.

Color. Body testaceous.

Head. Labral apex slightly to moderately emarginate medially. Clypeal apex straight or slightly emarginate. Frons with small punctiform fovea; microsculpture of isodiametric mesh. Mentum with prominent median tooth. Mentum and submentum separated by complete transverse suture. Ligula moderately wide but not laterally expanded at apex. Paraglossa slightly longer than ligula.

Thorax. Pronotum cordate; posterior angle prominent but rounded; lateral and basal beads complete; apical bead present laterally; microsculpture of isodiametric mesh or in

some specimens slightly stretched medially.

Legs. Foretibia with distal portion moderately expanded laterally; apical spur lanceolate. Hindfemur with 5 to 10 long setae on posterior margin. Hindtarsus with segment I approximately = to segment II and shorter than II + III.

Elytron. Intervals flat; interval III with dorsal setigerous puncture about 1/3 from apex; microsculpture of isodiametric mesh.

Hind wing. Full and apparently functional.

Abdomen. Sterna III to VI with numerous extra setae; sterna III to V with 1 pair of ambulatory setae each; sternum VI with 2 pairs of ambulatory setae. Tergum VIII of ♀ with broadly rounded apex.

Male genitalia. Median lobe with apex long, arising from right side and therefore slightly asymmetrical; membranous area of dorsum short, not reaching basal bulb; apical disc absent.

Female genitalia. Valvifer weakly sclerotized. Stylus weakly sclerotized and somewhat lobe like. Proctiger without normal setae but with many irregularly sclerotized plates.

*Discussion.* — Csiki (1932) lists 2 species in this endemic New Zealand genus: *fulvescens* Bates, 1874; and *novaezealandiae* (Castelnau), 1867. I have not been able to secure specimens of the latter species but suspect from its original description that it may be conspecific with *fulvescens*.

### 3 genus *Crasodactylus* Guérin-Ménéville (Fig. 181)

*Crasodactylus* Guérin-Ménéville, 1847: 258. [TYPE SPECIES: *Crasodactylus punctatus* Guérin-Ménéville, 1847, by monotypy].

*Description.* — Body length approximately 7.5 to 10 mm. Body with short moderately dense pubescence.

Color. Body black to dark piceous.

Head. Labral apex moderately to strongly emarginate medially. Clypeus with apex straight to slightly emarginate medially; raised transverse ridge present behind apex. Frons with fovea in *punctatus* punctiform and in many specimens fovea obscured by mainly non-setigerous punctures, in *indicus* fovea punctiform with clypeo-ocular prolongation and also in many specimens fovea obscured by mainly non-setigerous punctures; microsculpture obsolete. Antenna short, scarcely reaching pronotal base. Mentum without tooth or with slight median swelling in *punctatus*, with tooth in *indicus*. Mentum and submentum separated by complete transverse suture. Ligula narrow, not laterally expanded at apex. Paraglossa longer than ligula and curving behind it distally; dorsum and sides with moderately long pubescence.

Thorax. Pronotum (Fig. 181) suborbiculate in form, convex; posterior angle broadly rounded; lateral depression narrow; lateral and basal beads complete; apical bead present laterally; microsculpture obsolete.

Legs. Foretibia with distal portion moderately expanded laterally; apical spur lanceolate. Hindfemur with 2 long and various numbers of short setae on posterior margin. Hindtarsus with segment I shorter than II + III. Dorsum of all tarsi pubescent. Foretarsus of ♂ with apex of segment I in many specimens and all of segments II to IV in all specimens laterally expanded and spongy pubescent beneath. Midtarsus of most ♂♂ with segments II to IV slightly expanded laterally and each with patch of ventral spongy pubescence.

Elytron. Intervals slightly convex; moderately dense setigerous punctures covering surface in *punctatus*; setigerous punctures sparse and irregular on median portion but moderately dense on base, sides, and apex in *indicus*; microsculpture obsolescent except for irregular

weak isodiametric mesh apically.

Abdomen. Sterna with short dense pubescence; sternum VI of ♂ with 2 pairs of ambulatory setae; sternum VI of ♀ with median portion of apex slightly swollen as small plate-like disc somewhat as in *Cenogmus*.

Male genitalia. Median lobe with small apical disc.

Female genitalia. Valvifer strongly sclerotized and with several fine short distal setae; distal lateral margin deeply emarginate. Stylus with several fine short setae present proximally on apical segment. Proctiger on each side modified into sclerotized paddle-like structure free distally from tergum and with stout setae apically and laterally.

*Discussion.* — I have examined both sexes of the two species in the genus. The species *punctatus* Guérin-Meneville, 1847 inhabits sandy areas from western India south to the mountains of Kivu in the Belgian Congo and is also present on the Arabian peninsula (Andrewes, 1933; Basilewsky, 1950). The species *indicus* Andrewes, 1933 is cited in the original description as being found at several localities in western India.

4 genus *Cenogmus* Sloane  
(Figs. 174, 180, 205, 232, 238)

*Cenogmus* Sloane, 1898: 456, 457, 460. [TYPE SPECIES *Cenogmus castelnaui* Csiki, 1932: 1053, here designated, Csiki's replacement name for *Harpalus rotundicollis* Castelnau, 1867, preoccupied at time of original description by several other species in *Harpalus* named "rotundicollis"].

*Description.* — Body length approximately 8 to 10 mm. Body narrow and convex.

Color. Body rufopiceous to piceous.

Head. Labral apex moderately emarginate medially. Clypeal apex straight to moderately emarginate medially. Frons with fovea punctiform to elliptical, always small and with clypeo-ocular prolongation and in many specimens also with medio-posterior prolongation; microsculpture of isodiametric mesh. Gena wide, narrowest part between eye and mouth wider than maximum width of first antennal segment. Mentum without indication of a tooth in most specimens, some specimens with margin slightly swollen medially. Mentum separated from submentum by a complete transverse suture. Ligula elliptical in form and not expanded at apex (Fig. 174); side with small concave area distally. Paraglossa (Fig. 174) longer than ligula, hook shaped.

Thorax. Pronotum (Fig. 180) suboval in shape; posterior angle completely rounded; side with a prominent very flattened lateral depression sharply delimited from convex disc by discrete groove; lateral bead complete but fine; apical and basal beads present laterally, and in some specimens also medially; microsculpture of isodiametric mesh, but obsolescent medially in some specimens.

Legs. Foretibia with distal portion moderately expanded laterally; apical spur lanceolate. Hindfemur with 2 to several long setae on posterior margin. Hindtarsus with segment I shorter than II + III. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with apex of segment I in many specimens and all of segments II to IV in all specimens laterally expanded and spongy pubescent beneath.

Elytron. Intervals flat to slightly convex and with numerous small non-setigerous punctures; interval III with dorsal setigerous puncture about 1/4 way from apex; interval VII with very small ocellate puncture at extreme apex and large prominent ocellate puncture slightly more proximally located.

Abdomen. Sterna III to V with extra setae; sternum VI of ♂ with 2 pairs of ambulatory

setae; sternum VI of ♀ with distal margin enlarged medially to form prominent plate-like area in posterior view (Fig. 205).

Male genitalia. Median lobe with membranous area of dorsum relatively short, not reaching basal bulb, exact proximal boundaries not discernible; lacking apical disc.

Female genitalia. Valvifer (Fig. 232) moderately sclerotized and moderately convex, with several prominent distal setae; lateral dorsal margin connecting to membranous flap containing setae, flap joined to tergum. Stylus with basal segment bearing several setae on distal lateral and mesal margins. Spermatheca with distal annulated portion short and stout (Fig. 238).

*Discussion.* — This genus is well characterized by the prominent plate-like area on the distal margin of the female sixth abdominal sternum and the short, stout distal annulated portion of the spermatheca. The 3 currently recognized species together with their ranges are: *castelnaui* Csiki, 1932, Queensland, western Australia, and Tasmania; *interioris* (Castelnau), 1867, western Australia; and *opacipennis* (Chaudoir), 1878, south-western Australia. I have not obtained specimens of the latter species. Additional undescribed species may exist in Australia, and the species of the genus are in need of revision.

#### 5 genus *Hypharpax* MacLeay

*Hypharpax* MacLeay, 1825: 22. [as subgenus of *Harpalus*]. [TYPE SPECIES: *Harpalus* (*Hypharpax*) *lateralis*, MacLeay, 1825, by monotypy, = *dentipes* (Wiedeman, 1823): 54]. *Sagraemerus* Redtenbacher, 1868: 13. [TYPE SPECIES: *Sagraemerus javanus* Redtenbacher, 1868: 14, by monotypy, = *dentipes* (Wiedemann, 1823): 54].

*Description.* — Body length approximately 7 to 13 mm.

Color. Body black to dark piceous.

Head. Labral apex slightly to strongly emarginate medially. Clypeal apex straight to moderately emarginate medially. Frons with frontal fovea punctiform, with or without clypeo-ocular prolongation. Gena wide, narrowest part between eye and mouth wider than maximum width of first antennal segment in most specimens. Mentum with very prominent median tooth in most specimens, tooth only moderately prominent in some specimens. Mentum separated from submentum by complete transverse suture. Ligula narrow, not expanded at apex. Paraglossa slightly longer than ligula, removed distally from it.

Thorax. Pronotum with posterior angle broadly rounded in most species, sharp or acute in few species; lateral bead complete; apical and basal beads present at least laterally.

Legs. Foretarsus with distal portion moderately expanded laterally; apical spur lanceolate. Hindfemur with various numbers of long setae on posterior margin. Hindtarsus with segments stout; segment I not to slightly more than twice as long as wide at apex and always shorter than II + III. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with segments II to IV laterally expanded and spongy pubescent beneath or not laterally expanded and with small patch of spongy pubescence on venter of each segment.

Elytron. Intervals flat to convex; interval III with or without dorsal setigerous puncture; interval VII in most species with small ocellate puncture at extreme apex and large prominent ocellate puncture slightly more proximally located.

Hind wing. Full and apparently functional.

Abdomen. Sterna with varied number of setae.

Male genitalia. Median lobe lacking apical disc.

Female genitalia. Valvifer vestigial and very weakly sclerotized in most species. Stylus weakly sclerotized and with apical segment lobe like in most species. Proctiger absent or ves-



tigial in some species.

*Discussion.* — *Sagraemerus* was based on a species now known to be conspecific with the type species of *Hypharpax*. The genus *Hypharpax* is distributed from Tasmania, through Australia to New Guinea, Sumatra, Java, and the Celebes, and is also found in New Zealand. Most of the 30 known species are recorded from Australia. The species are: *abstrusus* Bates, 1878; *aerus* (Dejean), 1829 ♀\*; *antarticus* (Castelnau), 1867; *australis* (Dejean), 1829 ♂\*; *bostocki* (Castelnau), 1867 \*; *celebensis* Chaudoir, 1878 ♀\*; *dampieri* (Castelnau), 1867 (one badly damaged female seen, has segment I of hindtarsus = to II + III and probably belongs in subgenus *Anisotarsus*, additional material needs to be examined); *dentipes* (Wiedemann), 1823; *deyrollei* (Castelnau), 1867 ♀\*; *flavitaris* Chaudoir, 1878 \*; *flindersi* (Castelnau), 1867 ♂\*; *habitans* Sloane, 1898 \*; *inornatus* (Germar), 1848 \*; *interioris* Sloane, 1895 \*; *kingi* (Castelnau), 1895 \*; *krefti* (Castelnau), 1867; *moestus* (Dejean), 1829 ♂\*; *nitens* Sloane, 1910 \*; *obsoletus* Blackburn, 1892; *opacipennis* MacLeay, 1888 \*; *peroni* (Castelnau), 1867; *puncticollis* MacLeay, 1888 \*; *queenslandicus* (Csiki) 1932; *ranula* (Castelnau), 1867; *rotundipennis* Chaudoir, 1878; *sculpturalis* (Castelnau), 1867 ♂\*; *simplicipes* Chaudoir, 1878 \*; *sloanei* Blackburn, 1891 ♀\*; *varus* MacLeay, 1888 \*; and *vilis* Blackburn, 1891. The species *antarticus*, *flindersi* and *queenslandicus* listed as *Diaphoromerus* by Csiki (1932) actually belong in *Hypharpax* since they have stout, short hindtarsi, vestigial valvifer and stylus with lobe-like apical segment. The species of *Hypharpax* are not well understood and need revision.

#### 6 genus *Gnathaphanus* MacLeay

*Gnathaphanus* MacLeay, 1825: 20. [TYPE SPECIES: *Gnathaphanus vulneripennis* MacLeay, 1825, by monotypy.].

*Pachauchenius* MacLeay, 1864: 116. [TYPE SPECIES: *Pachauchenius laeviceps* MacLeay, 1864, by monotypy, = *philippensis* (Chevrolat), 1841].

*Mirosarus* Bates, 1878b: 319. [TYPE SPECIES: *Mirosarus insularis* Bates, 1878, by monotypy, = *melbournensis* (Castelnau), 1867].

*Description.* — Body length approximately 7 to 17 mm. Body slender to moderately stout.

Color. Various.

Head. Head often relatively large. Labral apex straight to slightly emarginate medially. Clypeal apex straight to moderately emarginate medially. Frons with fovea punctiform. Mentum with prominent tooth in most species. Mentum and submentum separated by complete transverse suture. Ligula narrow, not expanded at apex. Paraglossa slightly longer than ligula.

Thorax. Pronotum with posterior angle moderately to broadly rounded in most species; lateral bead complete; apical and basal beads present at least laterally.

Legs. Foretibia with distal portion moderately expanded laterally; apical spur lanceolate, angulate medially on each side, or swollen basally. Hindfemur in most specimens with 2 long setae on posterior margin. Hindtarsus with segments slender and elongate; first segment 3 to 6 times as long as wide at apex and longer than II + III. Fore- and midtarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Intervals flat to strongly convex; number of setigerous dorsal punctures and intervals on which such punctures located varied according to species, always however with at least 3 dorsal setigerous punctures on apical 1/3 to 1/4 of interval III; interval VII with small ocellate puncture at extreme apex and large prominent ocellate puncture slightly more proximally located.

Hind wing. Usually full and apparently functional.

Abdomen. Sternum VI with 1 or 2 pairs of ambulatory setae in ♂.

Male genitalia. Median lobe lacking apical disc.

Female genitalia. Valvifer moderately sclerotized, and in most species with few distal setae; shape various but distal lateral margin at least slightly emarginate in most species.

*Discussion.* — The species of this genus are concentrated in Australia; several also are present in Malasia and adjacent Asia; a few widely distributed species reach India, the Philippines and islands east to Samoa and New Caledonia; 2 species are recorded from China and 1 from the Ryukyu Islands of Japan. In addition, Habu (1973) has tentatively transferred *Iwosiopelus masaudai* Nakane and Ishida, 1959, found on the island of Iwo Jima, Japan, to the genus *Gnathaphanus*. I have not examined the single known specimen (a female) of this species, and Habu's transfer was only tentative. Therefore I have not included this species in the list of those belonging to *Gnathaphanus*. Darlington (1968) mentioned: "Of the 5 species known in New Guinea, all are shared with Australia and several are widespread also on the Malay Archipelago or islands of the western Pacific. These insects are often common in open country including grassland and open woodland, but are not often found in rain forest. All species of the genus that I know are fully winged and probably fly." The 25 currently recognized species are: *aridus* Blackburn, 1892\*; *chinensis* Schauburger, 1932\*; *chujoi* Habu, 1973\*; *denisonensis* (Castelnau), 1867\*; *froggatti* (MacLeay), 1888\*; *glamorgani* (Lequillon), 1841\*; *goryi* (Gory), 1833\*; *kansuensis* Schauburger, 1932\*; *herbaceus* Sloane, 1899\*; *latus* Sloane, 1899\*; *licinoides* Hope, 1842; *melbournensis* (Castelnau), 1867; *minutus* (Castelnau), 1867\*; *parallelus* Louwerens, 1962\*; *papuensis* (MacLeay), 1876\*; *philippensis* (Chevrolet), 1841; *picipes* (MacLeay), 1864; *pulcher* (Dejean), 1829; *punctifer* (Castelnau), 1867\*; *rectangulus* Chaudoir, 1878\*; *riverinae* Sloane, 1894; *sculpturalis* (Castelnau), 1867\*; *subolivaceus* (MacLeay) 1825; *upolensis* (Csiki), 1915; *vulneripennis* MacLeay, 1825; *whitei* Sloane, 1907. The species *glamorgani*, *goryi*, *minutus*, *papuensis*, and *sculpturalis* were listed as tentative members of the genus by Csiki (1932). The species of *Gnathaphanus* are poorly understood, and in need of revision.

*Pachauchenius* and *Microsarus* were monotypic genera each based on a form now regarded as conspecific with a species of *Gnathaphanus*.

#### 7 genus *Pseudanisotarsus* NEW GENUS

(Figs. 182, 239)

TYPE SPECIES: *Anisotarsus nicki* van Emden, 1953 here designated.

*Description.* — Body length 9.54 to 10.8 mm. Body form similar to that of subgenus *Anisotarsus*.

Head. Frons with fovea punctiform, obsolescent. Mentum lacking tooth. Mentum and submentum separated by complete transverse suture. Ligula narrow, not expanded at apex; with 4 to 5 distal dorsal setae. Paraglossa slightly longer than ligula.

Thorax. Pronotum (Fig. 182) with irregular series of setigerous punctures along lateral margin and along lateral portions of basal and apical margins.

Elytron. Intervals I, III, V, and VII each with row of setigerous punctures extended from base to apex and in most specimens situated along next odd stria; interval VII with small setigerous sub-ocellate puncture near apex and slightly more proximal ocellate puncture; intervals IX and X and apex of all intervals with numerous setigerous punctures.

Hind wing. Full and apparently functional.

Abdomen. Sterna with numerous extra setae of varied length; sterna III to V each with 1 pair of ambulatory setae; sternum VI of ♂ with 2 pairs of ambulatory setae.

Male genitalia. Median lobe with membranous area of dorsum reaching basal bulb; lacking apical disc but with apex prominently arrow shaped; apex concave just distal to end of dorsal membranous area. Everted internal sac with varied field of scales and spine-like scales.

Female genitalia. Valvifer (Fig. 239) reduced to small, weakly sclerotized transverse plate; apical portion membranous and without discrete boundaries. Stylus (Fig. 239) dorso-ventrally flattened, lobe like; apical and basal segments fused, separated by only faint groove; apical segment in many specimens with 1 to 2 short proximal setae. Proctiger absent.

*Discussion.* — This genus contains only *nicki*, originally described as a subspecies of *Notiobia* (*Anisotarsus*) *tucumana* by van Emden (1953) though it is clearly a separate species and also differs greatly from all members of *Notiobia* (*sensu lato*). The shape and symmetry of the median lobe as opposed to the asymmetric median lobe of *tucumana* is itself sufficient to warrant separate specific status for *nicki*. The peculiar punctuation of the elytron, setigerous punctures of the pronotum, and vestigial transverse valvifer, distinguish *nicki* from all species of *Notiobia* (*sensu lato*). In addition, the combination of 4 to 5 distal dorsal setae of the ligula, stylus with fused segments, and complete absence of proctiger distinguish *nicki* from all other species of the subtribe. Each of the last 3 characters is in itself sufficient reason to place *nicki* in a separate genus.

Since the species *nicki* has not been fully described, I am providing a description in this paper.

*Pseudanisotarsus nicki* NEW COMBINATION AND NEW STATUS

*Anisotarsus tucumanus nicki* van Emden, 1953: 520. [Probable paratype examined at BMNH (see discussion)].

*Description.*

Color. Dorsum with labrum dark piceous, lateral and apical margins of many specimens rufotestaceous to rufopiceous; remainder of head, pronotum, and elytron blue, bluish green, or green; relative darkness of head, pronotum, and elytron often varied in individual specimens. Venter rufopiceous to piceous, lateral portions often with violaceous, bluish, bluish-green, or green tinge.

Head. Labral apex strongly emarginate medially. Clypeal apex slightly emarginate medially. Supra-antennal ridges strongly convergent anteriorly. Frons with microsculpture of isodiametric mesh.

Thorax. Pronotum (Fig. 182) with side evenly curved towards posterior angle; posterior angle rounded; lateral depression obsolete; lateral bead complete; apical bead present laterally; basal bead complete or interrupted medially; basal fovea obsolescent; microsculpture of isodiametric mesh. Prosternum densely pubescent with moderately long setae.

Legs. Foretibia with apical spur lanceolate. Hindfemur with 8 to 20 long setae on posterior margin. Hindtarsus with segment I shorter than II + III. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Humerus rounded; subapical sinuation obsolescent; sutural angle broadly rounded; microsculpture of isodiametric mesh.

*Variation.* — I have not seen enough specimens to evaluate whether the observed variation is intra- or interpopulational.

*Discussion.* — The BMNH contains 1 male and 1 female of *nicki*. The male is labeled: "Type", "Argentina Prov. Buenos Aires 12.38. F. Shade", "Gesch. 3. 1939 von F. Schade", "nicki Emd type", "F. van Emden Bequest B. M. 1960-129". As van Emden stated "Bahia Blanca, Prov. Buenos Aires, xi. 46, ♂ type, 1 ♀ paratype (Ni.), 1 ♀ paratype (Emd.); Prov. Buenos Aires, xii. 38 (F. Schade), 1 ♂ paratype (Emd.)," the male bearing a type label at the BMNH is a paratype and not a holotype. From introductory information given by van

Emden "(Ni)" refers to "Dr. G. H. Nick, Sao Paulo (private collection)"; probably the holotype is in Brazil. The female specimen is labeled as being a paratype and as being collected at San Paulo, Brazil, but van Emden (1953) mentioned no specimens from Brazil.

The type labels on both the male and female specimens appear to be those used by van Emden (B. Brown, pers. commun.). Therefore, van Emden may have considered the male to be a holotype. I have noticed possible labeling errors in specimens of other species handled by van Emden so the exact status of the specimens at the BMNH can not be determined here.

Fortunately there is no confusion over the proper identification of *nicki* since van Emden illustrated its median lobe and described its pronotal, elytral and abdominal pubescence.

*Distribution.* — This species has been taken from areas in the Buenos Aires Province of Argentina. The female in the BMNH with the San Paulo label may be from San Paulo or possibly it may have been borrowed from a private collection housed at San Paulo and subsequently mislabeled.

*Material examined* (10 specimens)

#### ARGENTINA

PROVINCE BUENOS AIRES: Bahia Blanca, 2 ♂♂, 6 ♀♀, Hayward-Willimk (seen in private collection of J. Nègre, Versailles, France); no specified locality, 1 ♂, at BMNH labeled as described above.

#### BRAZIL

PROVINCE SAN PAULO: San Paulo, 1 ♀, (BMNH) (perhaps mislabeled as explained above).

#### 8 genus *Criniventer* van Emden

*Criniventer* van Emden, 1953: 519. [TYPE SPECIES: *Anisodactylus rufus* Brulle, 1838, by monotypy and original designation].

*Description.* — Body length approximately 9 mm. Body form as in subgenus *Anisotarsus*. Color. Body rufous to light rufopiceous. Legs and palpi testaceous.

Head. Frons with fovea obsolescent but with clypeo-ocular prolongation; microsculpture of isodiametric mesh. Mentum with prominent tooth. Mentum and submentum separated by complete transverse suture. Ligula strongly expanded laterally at apex. Paraglossa slightly longer than ligula.

Thorax. Pronotum strongly cordate; lateral depression broadly concave and sharply delimited from disc; lateral part of apex with setigerous punctures; base and apex with prominent non-setigerous punctures.

Legs. All femora pubescent. Hindtarsus with segment I shorter than II + III. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with segments not laterally expanded but with sparse spongy pubescence on venter of apex of segment I and all of II and III.

Elytron. Scutellar stria vestigial to absent; odd and in some specimens also even intervals with irregular row of fine, short setae; subapical situation absent.

Abdomen. Sterna with irregular short pubescence; sternum VI of ♂ with 1 pair of ambulatory setae.

Male genitalia. Median lobe with membranous area of dorsum extended to basal bulb; lacking apical disc.

*Discussion.* — This genus contains only the species *rufus* which is reported by van Emden

(1953) as occurring in Argentina, Chile and Uruguay. I have seen 3 males but not females.

### 9-11 genus *Notiobia* Perty

*Notiobia* Perty, 1830: 13. [TYPE SPECIES: *Notiobia nebrionides* Perty, 1830, by monotypy].

*Description.* — Body length 6.3 to 14.1 mm. Body form slender to moderately stout.

Head. Labral apex straight to prominently emarginate medially. Clypeus with apex straight, sinuate, or broadly emarginate medially, base of labrum exposed in many specimens with broadly emarginate apex. Frons with isodiametric microsculpture, obsolescent medially in some specimens. Mentum with prominent median tooth except in members of *tucumana* lineage. Mentum and submentum separated by complete transverse suture. Paraglossa slightly longer than ligula.

Thorax. Pronotum varied in shape; lateral depression absent to prominent; lateral bead complete but varied in prominence; apical and basal beads present at least laterally; basal and outer fovea various; microsculpture of isodiametric mesh, slightly stretched transversely or obsolete medially in some specimens. Pubescence of venter various.

Legs. Foretibia with apical spur lanceolate, slightly curved in some specimens. Hindfemur with 2 to 12 long setae on posterior margin. Hindtarsus with segment I shorter than II + III.

Elytron. Scutellar stria elongate in *umbrata* and *umbrifera*; microsculpture of isodiametric mesh in most specimens.

Hind wing. Full and apparently functional in most species, vestigial in *hilariola*, dimorphic in *cyanippa*.

Abdomen. Sterna with extra setae in species of the *tucumana* lineage of subgenus *Anisotarsus*; sternum VI of ♂ with 1 or 2 pairs of ambulatory setae. Apex of tergum VIII of ♀ various.

Male genitalia. Median lobe symmetrical except in *tucumana*; membranous area of dorsum extended to basal bulb except in *leiroides* and *parilis*; without apical disc in *Anisotarsus* and *Notiobia*, with apical disc in *Diatypus*.

Female genitalia. Valvifer flat to slightly convex; lateral margin semi-membranous and without distinct boundary; apex with or without several setae (Fig. 129). Stylus varied in shape.

*Discussion.* — Previous authors have simply assumed *Notiobia* (s. str.) and *Anisotarsus* to be distinct genera. The only paper providing any information on possible differences between the two groups is that of van Emden (1953) who provided a key to the genera of Neotropical Anisodactylina. The characters utilized by him in the key to separate the two groups can be tabulated as follows:

#### *Notiobia*

Frontal impression large and deep, usually with clypeo-ocular prolongation which reaches eye. If clypeo-ocular prolongation absent, then supra-antennal ridges conspicuously divergent from middle of eyes to antennal insertion. Frons and vertex not very convex. Eye large and very convex. Pronotum always cordate, though often with obtuse posterior angle.

#### *Anisotarsus*

Frontal impression small and shallow. Supra-antennal ridges varied, if divergent from middle of eyes to antennal insertion, then gena wider than first antennal segment. Frons and vertex strongly and evenly convex. Eye rather small, moderately convex and not much protruding. Prothorax more often with side arcuate to posterior angle.

The above characters do not seem stable enough to warrant generic separation of *Notiobia* (*s. str.*) and *Anisotarsus* on phenetic grounds. In *Anisotarsus* the frontal fovea is always small, shallow and without a clypeo-ocular prolongation. While the frontal fovea in *Notiobia* (*s. str.*) is usually deep and large and with a clypeo-ocular prolongation, it does vary considerably. For example: *parilis* has a large, deep frontal fovea lacking a readily visible clypeo-ocular prolongation; *leiroides* has a moderately wide deep fovea lacking a clypeo-ocular prolongation; *obscura* has a relatively smaller and shallower fovea bearing a faint, short clypeo-ocular prolongation which does not reach the eye; *limbipennis* has a relatively large deep fovea bearing a prominent clypeo-ocular prolongation which reaches the eye; *disaparilis* has a relatively large, deep frontal fovea which usually lacks any indication of a clypeo-ocular prolongation; *umbrifera*, *umbrata*, *melaena*, *wilkensi*, and *cooperi* have moderately wide deep fovea each bearing a clypeo-ocular prolongation which reaches the eye; *incerta* and *chiriquensis* have relatively small, shallow fovea each bearing a prominent clypeo-ocular prolongation which reaches the eye; and *cupreola* has a moderately wide fovea bearing a clypeo-prolongation of varying prominence and length.

The degree of divergence of the supra-antennal ridges also varies in *Notiobia* (*s. str.*). This variation does not appear to be correlated with the condition of the frontal fovea except that species completely lacking a clypeo-ocular prolongation have the supra-antennal ridges strongly divergent anteriorly. Within the *Anisotarsus* group, the species *cyanippa* and *brevicollis* have strongly divergent supra-antennal ridges while in *praeclara* the ridges vary from slightly to strongly divergent, and in *cupripennis* they are moderately divergent. The remaining species within the *Anisotarsus* group have the supra-antennal ridges not or only slightly divergent.

I have not been able to recognize the difference in convexity of the frons and vertex which van Emden described.

The pronotum in *Notiobia* (*s. str.*) is strongly cordate in many species such as *parilis*, *disaparilis* and *limbipennis*, but it is more evenly rounded from apex to base in other species such as *chiriquensis* and *ewarti*.

The eye of species of *Notiobia* (*s. str.*) and of the *Anisotarsus* group varies in relative size, convexity, and protrusion from the side of the head. In general, species of *Notiobia* have a relatively larger and more protruding eye, but there are many exceptions to this rule.

In addition to distinguishing characters given by van Emden the base of the pronotum is lobed in most species of *Notiobia* (*s. str.*) and non-lobed in most species of *Anisotarsus*.

In my opinion, these characters are not sufficient to separate the two groups as genera. I believe, however, that they are sufficient to warrant separate subgeneric status for each, and I here treat *Anisotarsus* as a subgenus of *Notiobia*.

*Diatypus* has until now been treated as a separate genus. However, I believe it has evolved from the same ancestor as has the subgenus *Notiobia*. I do not think species of *Diatypus* are phenetically different enough from those of *Notiobia* and *Anisotarsus* to warrant separate generic status. Species of *Diatypus* possess the same form of valvifer as found in species of *Notiobia* and *Anisotarsus*. And species of *Diatypus* agree with all species of *Notiobia* and most species of *Anisotarsus* in having a median mental tooth. In addition, the species of *Diatypus* (except for a few members of the "*Paradiatypus*" species group which have secondarily reverted to the plesiomorphic condition of small eye and wide gena) and those of *Notiobia* share the clearly apomorphic feature of narrow gena and large protruding eye. The only constant differences between species of *Diatypus* and of *Notiobia* and *Anisotarsus* are the possession by *Diatypus* species of extra dorsal setigerous punctures on the third elytral interval and an apical disc on the median lobe of males. These phenetic differences do not warrant separate generic status for *Diatypus*. However they do seem sufficient for subgen-

eric status. Therefore I am here proposing to treat *Diatypus* as a subgenus of *Notiobia*.

### 9 subgenus *Anisotarsus* Chaudoir NEW STATUS

*Anisotarsus* Chaudoir, 1837: 41. [TYPE SPECIES: *Anisotarsus brevicollis* Chaudoir, 1837, designated by van Emden, 1953: 519].

*Diaphoromerus* Chaudoir, 1843 a: 402. [TYPE SPECIES: *Diaphoromerus iridipennis* Chaudoir, 1843: 405, by monotypy. NEW SYNONYMY].

*Eurytrichus* LeConte, 1848: 287 [page incorrectly numbered "387" in paper]. [TYPE SPECIES: *Feronia terminata* Say, 1823, designated by van Emden, 1953: 525].

*Stilbolidus* Casey, 1914: 171, 206. [TYPE SPECIES: *Harpalus mexicanus* Dejean, 1829, by original designation of Casey, p. 206-207].

*Description.* — Body length 5.3 to 14.1 mm.

Color. Various except antenna with distal 8 to 9 segments of most specimens each with longitudinal median dark bar.

Head. Frontal fovea small to obsolete and lacking clypeo-ocular prolongation. Eye small to large and protruding. Width of narrowest part of gena relative to maximum width of first antennal segment various; supra-antennal ridges varied from not divergent to strongly divergent anteriorly.

Thorax. Pronotum semi-rectangular; not strongly narrowed at base in most species. Venter, except for apex of prosternal lobe, glabrous unless otherwise noted.

Legs. Unless otherwise stated, ♂ fore- and midtarsi with apex of segment I and all of segments II - IV laterally expanded and spongy pubescent beneath. Hindfemur with 2 to 4 long setae on posterior margin in most species, 4 to 12 in members of *tucumana* lineage. Hindtarsus with segments slender and elongate; first segment 3 to 4 times as long as wide at apex and slightly shorter to slightly longer than II + III.

Elytron. Interval III, with 1 or 2 dorsal setigerous punctures; interval VII, unless otherwise stated, with small subocellate puncture (may be difficult to see) near apex and slightly more proximal larger ocellate punctures; microsculpture of isodiametric mesh unless otherwise stated.

Hind wing. Full and apparently functional in most species, vestigial in *hilariola*, dimorphic in *cyanippa*.

Abdomen. Sternum VI of ♂, unless otherwise noted, with 1 pair of ambulatory setae.

*Discussion.* — Blatchley (1910) in his pioneering work on the beetles of Indiana treated the 3 species found there as members of the genus *Anisodactylus*. Casey (1914) split *Anisotarsus* into 2 separate genera and then in 1924 proposed many new species which are today regarded as conspecific with previously described ones. Van Emden (1953) revised all the species and regarded *Anisotarsus* as a valid separate genus. However, he was mainly interested in the Neotropical fauna, he apparently had available only small series of most species, and he did not examine types deposited in North America. Consequently he failed to see crucial intergrades between various forms and was not able to properly assign synonyms to those species he recognized as valid. These errors are especially prominent in his treatment of the North American species. Lindroth (1968) in his fine work on the Carabidae of Canada and Alaska revised the 3 species found in Canada and also keyed out 3 others not occurring there. However, since he was primarily interested in northern forms, a complete revision of all the North American species together with an examination of the relationship of *Anisotarsus* to other supra-specific taxa is warranted. As discussed for the genus *Notiobia*, I feel that *Anisotarsus* is merely a subgroup of that genus. *Anisostichus* proposed by van Emden (1953) as a new subgenus of *Anisotarsus* is in my opinion a valid separate genus as discussed

under that taxon.

*Diaphoromerus* has until now been treated as a separate genus composed of species found in the Australian Region. However, E. Zimmerman while working on the Coleoptera of the Hawaiian Islands found several introduced species of *Diaphoromerus* there and therefore investigated the genus *Diaphoromerus*. He concluded that the species of *Diaphoromerus* are not sufficiently different in morphological characters from those of *Anisotarsus* (*s. str.*) to warrant separate generic status (pers. commun. to G. E. Ball). I agree with this conclusion since the only appreciable morphological differences between species of *Diaphoromerus* and *Anisotarsus* (*s. str.*) are: in members of *Anisotarsus* (*s. str.*) the dorsal membranous area of the median lobe is elongate and reaches the basal bulb and also segment I of the hindtarsus of most specimens is usually shorter than II + III; in members of *Diaphoromerus*, the length of the dorsal membranous area of the median lobe and the relative lengths of the first 3 segments of the hindtarsus vary. These differences certainly are neither constant nor fundamental. Therefore, I treat *Diaphoromerus* as congeneric with the subgenus *Anisotarsus*.

For convenience of workers studying the fauna of the New World and Australian Region the species of *Anisotarsus* may be grouped respectively into the "*Anisotarsus*" and "*Diaphoromerus*" species groups. The North American species of the "*Anisotarsus*" species group are revised in this paper. The remaining named forms of this group are found in temperate areas of South America and are: *bradytoides* (H. W. Bates, 1891; *tucumana* (Dejean, 1831; *peruviana* (Dejean), 1829; *elata* (Erichson), 1847; *margaretæ* (van Emden), 1953; *stübeli* (van Emden), 1953; *præclara* (Putzeys), 1878; *cupripennis* (Germar), 1824; *latiusculus* (van Emden), 1953; *schnusei* (van Emden), 1953; *chalcites* (Germar), 1824; *amethystina* (Dejean), 1829. I have seen only males of *amethystina* but have examined both males and females of all the other named forms of South American *Anisotarsus*.

The "*Diaphoromerus*" species group is centered in Australia but has species also on New Zealand, New Guinea, New Caledonia, the Moluccas, and Timor; several of its species have also been introduced into the Hawaiian Islands. The 31 named forms of this group are: *angustula* (Chaudoir), 1878; *australasie* (Dejean), 1829; *basilewski* (Louwerens), 1962 ♂\*; *edwardsi* (Castelnau), 1867 ♀\*; *flavipalpis* (MacLeay), 1864 ♀\*; *germari* (Castelnau), 1867; *inaequalipennis* (Castelnau), 1867; *iridipennis* (Chaudoir), 1843; *lapeyrousei* (Castelnau), 1867; *laticollis* (MacLeay), 1888\*; *ludicollis* (Dejean), 1829; *melanara* (Dejean), 1829; *nigrans* (MacLeay), 1888\*; *oblongiuscula* (Castelnau), 1867\*; *opaca* (MacLeay), 1888; *ovata* (Chaudoir), 1878\*; *papuella* (Darlington), 1968; *papuensis* (Darlington), 1968; *patrueloides* (Castelnau), 1867; *perater* (Sloane), 1920\*; *planiuscula* (Chaudoir), 1878\*; *planoimpressa* (Castelnau), 1867 ♀\*; *polita* (MacLeay), 1888\*; *porcatula* (MacLeay), 1888\*; *quadricollis* (Chaudoir), 1878\*; *queenslandica* (Csiki), 1932; *rectangula* (Chaudoir), 1878; *rugosipennis* (Castelnau), 1867\*; *sculptipennis* (Castelnau), 1867\*; *sericipennis* (MacLeay), 1888\*; *viridipennis* (Sloane), 1920\*. The species *basilewski* is here transferred from the genus *Gnathaphanus* to the *Diaphoromerus* group of the subgenus *Anisotarsus*.

Members of the "*Diaphoromerus*" species group and the South American forms of the "*Anisotarsus*" species group are poorly understood and need revision.

### Key to the North American Species of the Subgenus *Anisotarsus*

#### *Notes concerning the key.*

This section discusses the more difficult to understand characters used in the key. The user of this key will soon note that many species key out in more than one couplet. Each of the species of *Anisotarsus* is highly variable, and usually it is not possible to distinguish a given species on the basis of one or two constant characters as in *Notiobia* and *Gynandrotarsus*. Rather, most species of *Anisotarsus* must be separated by a complex of characters



any one of which may be absent or highly modified on individual specimens.

The width of the narrowest part of the gena between the raised bead along the ventral edge of the eye and the mouth cavity relative to the maximum width of the first antennal segment is used in the first couplet. Species in which these widths are not closely correlated are treated in both halves of the couplet.

Body color is used extensively in the key. The color of a particular part of the body is generally easy to determine for a given specimen. However, in some species various body regions may exhibit faint to prominent metallic reflections or tinges in addition to their basic color. Illumination produced by an incandescent lamp is suitable for examination of these tinges, except for specimens keying to couplet 2 for which daylight or equivalent fluorescent light should be used. The perception of some tinges is affected by the angle at which light strikes the specimen; therefore a specimen being examined for a given tinge should be held under the microscope at several different angles. Particular care must be exercised when the specimen is teneral as characteristic tinges may be faint or even absent. Also, a specimen being examined for a tinge should first be cleaned by soaking it in hot detergent solution in order to remove grease and dirt, then rinsed to remove the detergent.

Body size has been used in several couplets and in each instance has been measured as described in the "Measurements" section.

The shape and structure of the median lobe are employed to separate species in several couplets. In some of these couplets mention is made of a prominent internal sac spine being visible beneath the membranous surface of the dorsum or in a few instances also projecting out into the ostium. In order to observe this spine, it is usually necessary to completely wet the median lobe by immersing it in boiling water. In some cases it may also be necessary to soak the median lobe in hot potassium hydroxide for approximately 1 minute in order to darken the spine and make the membranous area of the dorsum more transparent.

In order to construct a key which is not excessively long and which will separate all specimens encountered, I give geographical distribution in couplets 15, 16, 18 and 23. In these 4 couplets the ranges of the species being compared are either far removed from one another or else are used only as subsidiary aids after morphological characters separating the species have been provided.

Problems may be encountered in separating some specimens of *terminata* from *purpurascens*. Specimens of *terminata* which have a prominent lateral depression on the pronotum are easily separated in the key from *purpurascens* since the latter species never has this character.

Most specimens of *terminata* have a conspicuous greenish, aeneous, or cupreous tinge on the elytra while specimens of *purpurascens* completely lack such tinges or in a very few specimens have a faint greenish blue tinge. However, occasional specimens of *terminata* from southeastern United States, Mexico and Central America lack these tinges on the elytra and have at most a slight lateral depression on the pronotum. These specimens key to couplet 18. To reliably identify specimens keying to this couplet all sections of each half of the couplet should be read and compared.

*Key to the North American Species of the Subgenus Anisotarsus*

- |       |  |   |
|-------|--|---|
| 1     | Narrowest part of gena at least as wide as maximum width of first antennal segment ..... | 2 |
| —     | Narrowest part of gena not as wide as maximum width of first antennal segment .....      | 6 |
| 2 (1) | Elytron with brassy, greenish, aeneous, or cupreous tinge or coloration ....             | 3 |
| —     | Elytron without indication of such tinges or coloration .....                            | 4 |
| 3 (2) | Posterior angle of pronotum rounded (Fig. 8); median lobe (Figs. 89, 90)                 |   |

- with moderately long tapering apex, prominent spine visible beneath membrane of dorsum near ostium and projected into ostium ..... (in part) *hilariola* (H. W. Bates), p. 302
- Posterior angle of pronotum not rounded (Fig. 1); median lobe (Figs. 77, 78) with shorter, blunter apex, lacking prominent spine ..... *lamprota* (H. W. Bates), p. 318
- 4 (3) Pronotum with posterior angle subdentate (only on one side in some specimens), projected latero-posteriorly and lateral bead thick especially posteriorly (Fig. 5); median lobe without large internal spine ..... *mexicana* (Dejean), p. 320
- Pronotum with posterior angle obtusely rounded to nearly acute, not subdentate and lateral bead not thick (Figs. 6, 14); median lobe with prominent spine visible in membranous area of dorsum ..... 5
- 5 (4, 19) Pronotum with posterior angle rounded (Fig. 6); apex of abdominal sternum VI with 1 pair of ambulatory setae in ♂; hind wing vestigial in most specimens, full in some specimens ..... (in part) *cyanippa* (H. W. Bates), p. 302
- Pronotum with posterior angle right or slightly obtuse (Fig. 14); apex of abdominal sternum VI with 2 pairs of ambulatory setae in ♂; hind wing full ..... *brevicollis* (Chaudoir), p. 300
- 6 (1) Elytron with conspicuous greenish, brassy, or aeneous tinge ..... 7
- Elytron lacking conspicuous greenish, brassy, or aeneous tinge ..... 11
- 7 (6) First segment of antenna with central portion black or piceous, apices lighter in some specimens; dorsum of hind tarsus black or piceous; median lobe as in Figs. 89, 90 ..... (in part) *hilariola* (H. W. Bates), p. 302
- First segment of antenna testaceous, rufotestaceous, or rufous; dorsum of hind tarsus same color as first segment of antenna, except darker in some specimens of *virescens* ..... 8
- 8 (7) Head with eye reduced and not strongly protruding (Fig. 39) ..... (in part) *nitidipennis* (LeConte), p. 305
- Head with eye large and strongly protruding (Fig. 38) ..... 9
- 9 (8) Pronotum with prominent lateral depression originating near anterior angle and rapidly widened posteriorly, side broadly flattened in region of posterior angle (Figs. 10, 11); dorsum of hind tarsus testaceous or rufotestaceous. .... (in part) *terminata* (Say), p. 313
- Pronotum with lateral depression absent or if present prominent only in region of lateral seta, side not broadly flattened in region of posterior angle (Figs. 2, 12, 13) ..... 10
- 10 (9) Median lobe with apex sharply pointed in dorsal view (Figs. 61, 63, 65); dorsum of hind tarsus testaceous to rufotestaceous; microsculpture of pronotum of normal isodiametric mesh; range United States to Panama ..... (in part) *terminata* (Say), p. 313
- Median lobe with apex bluntly rounded in dorsal view (Fig. 69); dorsum of hind tarsus testaceous, rufotestaceous, rufopiceous, piceous, or black; microsculpture of pronotum consisting of extremely prominent isodiametric mesh; range central Mexico ..... (in part) *virescens* (Dejean), p. 308
- 11 (6) Body brown to piceous brown, or rarely piceous, without metallic tinges; AND microsculpture of pronotum obsolete medially; AND abdominal sternum VI with 2 pairs of ambulatory setae in both sexes ..... *picea* (LeConte), p. 309
- Combination of characters not as above ..... 12
- 12 (11) Pronotum with prominent lateral depression rapidly widened posteriorly, side broadly flattened in region of posterior angle (Figs. 9, 10) ..... 13
- Pronotum with lateral depression absent or if present prominent only near lat-

- eral seta, side not broadly flattened in region of posterior angle (Figs. 2, 3, 4, 6, 12, 16) ..... 14
- 13 (12) Dorsum of hind tarsus black or piceous; median lobe with blunt apex in dorsal view (Fig. 83) ..... (in part) *maculicornis* (Chaudoir), p. 307
- Dorsum of hind tarsi testaceous, rufotestaceous, or rufous; median lobe with tapered apex in dorsal view (Fig. 61) ..... (in part) *terminata* (Say), p. 313
- 14 (12) Dorsum of hind tarsus testaceous or rufotestaceous ..... 15
- Dorsum of hind tarsi piceous or black ..... 19
- 15 (14) Head with eye reduced, not prominent (Fig. 39); posterior angle of pronotum projected in some specimens (Fig. 16); range Canada and eastern United States ..... (in part) *nitidipennis* (LeConte), p. 305
- Head with eye large, prominent (Fig. 38); posterior angle of pronotum not projected; range southern United States and Mexico ..... 16
- 16 (15) Median lobe with short blunt apex in dorsal view (Fig. 71); body brown to reddish brown; pronotum without outer fovea; first antennal segment testaceous to rufous; range Guadalupe Island, southern tip of Baja California, and Mazatlan region of western Mexico ..... *flexilis* (LeConte), p. 310
- Median lobe with apex various; body color of most specimens not brown or reddish brown; pronotum with or without fovea; range California, Arizona, eastern United States, eastern and Central Mexico; OR if specimen from southern tip of Baja California then first antennal segment with central portion along posterior margin black or dark piceous, apices lighter in some specimens ..... 17
- 17 (16) Median lobe with blunt apex in dorsal view (Fig. 69); head and pronotum in most specimens with prominent greenish or purplish tinge; microsculpture of head and pronotum of prominent, sub-granulate isodiametric mesh ..... (in part) *virescens* (Dejean), p. 308
- Median lobe with apex tapered in dorsal view (Figs. 63, 65, 67); head and pronotum without prominent greenish or bluish tinge, with or without purplish or slight greenish tinge; microsculpture of head and pronotum of normal isodiametric mesh, not sub-granulate ..... 18
- 18 (17) Elytron piceous to rufopiceous, in some specimens with slight cupreous tinge, not with purple coloration; AND specimen from southeastern United States (as far west as eastern Arizona), Mexico, or Central America; AND pronotal sides various posteriorly; AND median lobe more slender in dorsal view (Figs. 63, 65) ..... (in part) *terminata* (Say), p. 313
- Elytron purplish, purplish-piceous, bluish or purplish black; AND specimen from California, Arizona, Gulf region of southeastern United States, or Mexico; AND pronotal sides strongly convergent posteriorly (Fig. 3); AND median lobe stouter in dorsal view (Fig. 67) ..... *purpurascens* (H. W. Bates), p. 311
- 19 (14) First segment of antenna testaceous, rufotestaceous, or rarely rufopiceous ..... 20
- First segment of antenna with central area black, dark piceous and in some specimens apices lighter; or first segment, infuscated along center of posterior edge ..... 5
- 20 (19) Head with eye reduced and not strongly protruding (Fig. 39); specimen from Canada or United States ..... (in part) *nitidipennis* (LeConte), p. 305
- Head with eye large and strongly protruding (Fig. 38); or if eye not large and

- protruding specimen from central or southern Mexico . . . . . 21
- 21 (20) Posterior angle of pronotum rounded (Figs. 2, 6); pronotum and elytron purplish black, bluish black or purple; side of pronotum not sinuate before posterior angle; hind wing vestigial or full . . . . . 22
- Posterior angle of pronotum subdentate or right (Figs. 4, 9) and side of pronotum of some specimens sinuate before posterior angle; pronotum and elytron black or piceous; hind wing full . . . . . 23
- 22 (21) Median lobe with prominent spine projected from ostium (Fig. 87); hind wing of most specimens vestigial; pronotum with sides more strongly convergent posteriorly and posterior angle of most specimens more broadly rounded (Fig. 6); microsculpture of pronotum of normal isodiametric mesh, disc in many specimens shiny, especially in ♂ . . . . . (in part) *cyanippa* (H. W. Bates), p. 302
- Median lobe without spine projected from ostium (Fig. 69); hind wing full; pronotum with sides less strongly convergent posteriorly and posterior angle of most specimens less broadly rounded (Fig. 2); microsculpture of pronotum of very prominent sub-granulate isodiametric mesh, disc not shiny . . . . . (in part) *virescens* (Dejean), p. 308
- 23 (21) Abdominal sternum VI with 2 pair of ambulatory setae in ♂; body length 8.3 to 9.5 mm.; range central Mexico . . . . . *schlingeri* new species, p.
- Abdominal sternum VI with 1 pair of ambulatory setae in ♂; body length 12.7 to 13.1 mm.; range southeastern United States . . . . . (in part) *maculicornis* (Chaudoir), p. 307

9.1 *Notiobia* (*Anisotarsus*) *brevicollis* (Chaudoir)  
(Figs. 14, 85, 86, 139)

*Anisotarsus brevicollis* Chaudoir, 1837: 42. [Lectotype (MNHP), here designated, ♀ labeled: "Puebla.", "Ex Musaeo Chaudoir", "Bates vidit 1881". Label added stating: "LECTOTYPE *Anisotarsus brevicollis* Chaudoir By G.R. Noonan". TYPE LOCALITY: Mexico originally cited by Chaudoir, here restricted to state of Puebla, Mexico].

*Anisotarsus laeviusculus* Chaudoir, 1837: 43. [Lectotype (MNHP), here designated, ♂ labeled: "Ex Musaeo Chaudoir". Label added stating: "LECTOTYPE *Anisotarsus laeviusculus* Chaudoir By G.R. Noonan". TYPE LOCALITY: Mexico as originally cited.

*Description.* — Body length 8.2 to 14.1 mm.

Color. Dorsum piceous to black, slightly shiny in some specimens; lateral margins of labrum and elytral epipleura somewhat lighter in many specimens. Venter, legs, and palpi rufopiceous to black. First segment of antenna with center black or piceous and in some specimens apices lighter, or rarely first segment with center of posterior margin infuscated to black and remainder lighter.

Head. Labral apex slightly to moderately emarginate medially. Clypeal apex slightly to moderately broadly emarginate medially. Frons as in *terminata*. Width of narrowest part of gena equal to or greater than maximum width of first antennal segment.

Thorax. Pronotum (Fig. 14) with posterior angle prominent, slightly obtuse to very slightly projected; lateral depression narrow, obsolescent to moderate; basal bead complete; microsculpture of isodiametric mesh. Prosternum glabrous medially, in some specimens with fine short scattered pubescence elsewhere. Mesosternum glabrous in most specimens, sparsely finely pubescent in others. Metasternum with scattered setae in region of midcoxa.

Legs. Dorsum of tarsi moderately to densely pubescent.

Elytron. Humerus angulate, in most specimens with small tooth; intervals flat; interval I in most specimens with 1 or more apical setigerous punctures; interval II with setigerous puncture about 1/3 forward from apex; subapical sinuation slight to moderate; sutural angle rounded.

Abdomen. Sternum VI with 2 pairs of ambulatory setae in ♂.

Male genitalia. Median lobe (Figs. 85, 86) relatively stout; apex short, bluntly rounded at tip, bent ventrad. Internal sac in repose with large prominent spine visible beneath membranous area of dorsum; everted sac with the large spine proximal to median lobe and with distal field of enlarged scales.

*Variation.* — Intrapopulational variation occurs in: body size and color; emargination of labral and clypeal apices; width of gena; prominence of pronotal posterior angle; prominence of pronotal lateral depression; pubescence of prosternum; and prominence of elytral subapical sinuation.

*Discussion.* — The description of *laeviusculus* immediately follows the description of *brevicollis*; Chaudoir noted the resemblance but stated *laeviusculus* to be more narrow and convex. Van Emden (1953) correctly treated *laeviusculus* as conspecific with *brevicollis*.

*Flight.* — Members of this species have not been taken at light or observed flying.

*Bionomics.* — Members of this species have been taken from January to November and at altitudes from 1,550 to 9,030 feet.

Within the United States this species appears to be restricted to forests predominantly of pine, oak, and possibly walnut, in mountainous areas of Arizona, New Mexico, and Texas. During the nights of September 4 and 5, 1969, I collected a total of 52 specimens at the Southwest Research Station, 5 mi. W. Portal, Arizona, which were found along a trail leading to a small creek. They did not seem however to be associated with the creek and were found no closer to it than approximately 5 yards. They were restricted to a portion of the trail shaded by pines and oaks during part of the day. The ground in the collecting area had scattered short grass and leaves on it and was bare in spots. The beetles were observed resting on the surface, crawling over the ground and mating. One female was seen eating the remains of a scarab head. No specimens were found along the trail during daylight hours.

Elbert Sleeper provided me with information on the vegetation in the La Laguna area of Baja California, and it is clear from his information that the species occurs there in the Lagunan Woodland as defined by Axelrod (1958).

Within mainland Mexico *brevicollis* occurs in a wide variety of habitats. Ball's data indicate it has been taken on the ground under debris or rocks in: forests of oak, pine, madrone and manzanita, and mixture of sycamore and walnut; along the edges of agricultural areas such as cornfields and sugar cane fields; along roadsides; in pastures and meadows; and by pools or streams in a variety of different habitats. It has also been taken: in cut-over tropical deciduous forest 9.5 mi. W. Morelia, 6,250 feet; in *Eucalyptus* woods in Mexico City; and under stones on open ground in an area with remains of cloud forest adjacent to intact cloud forest at Omiltemi, 7,300 feet. Specimens were taken by D.R. Whitehead in pinyon pine country 15.7 mi. W. Durango on January 11, when the ground was frosted. The beetles were aggregated under large rocks near pools adjacent to a stream.

*Distribution and material examined* (807 specimens). This species is centered in mainland Mexico but extends into mountainous areas of Arizona, New Mexico, Texas, and the Sierra Lagunas of southern Baja California (Fig. 139).

### 9.2 *Notiobia (Anisotarsus) cyanippa* (H. W. Bates)

(Figs. 6, 87, 88, 140)

*Anisotarsus cyanippus* H. W. Bates, 1882: 51. [Lectotype (BMNH), here designated, ♂ labeled: "Type H. T.", "Cuernavaca", "Mexico, Salle Coll.", "B.C.A. Col. I. 1. Anisotarsus cyanippus Bates ♂". Labels added stating: "Lectotype" and "LECTOTYPE Anisotarsus cyanippus Bates By G. R. Noonan". TYPE LOCALITY: Cuernavaca and Capulalpam, Mexico originally cited, here restricted to Cuernavaca, Morelos, Mexico].  
*Description.* — Body length 10.1 to 13.3 mm.

Color. Dorsum black, bluish black, or purplish black, shiny in many specimens. Venter and legs rufopiceous to black. Palpi rufopiceous to piceous. Antenna with first segment infuscated to black along at least central posterior margin.

Head. Labral apex slightly to moderately emarginate medially. Clypeal apex straight to slightly broadly emarginate medially. Frons as in *terminata*. Gena as in *brevicollis*.

Thorax. Pronotum (Fig. 6) with posterior angle obtusely rounded; lateral depression shallow or obsolescent, especially posteriorly; lateral bead prominent; basal bead complete; basal and outer fovea various; microsculpture of isodiametric mesh. Venter as in *brevicollis*.

Legs. Dorsum of tarsi moderately to densely pubescent.

Elytron. Humerus somewhat angulate; microsculpture in ♂ of isodiametric mesh becoming granulate laterally, in ♀ of granulate isodiametric mesh; remainder as in *terminata*.

Male genitalia. Median lobe (Figs. 87, 88) with apex short, slightly removed to right in dorsal view. Internal sac in repose with prominent spine visible beneath dorsum in region of ostium, in some specimens this spine projected through ostium.

*Flight.* — Most specimens examined had vestigial wings, but 3 specimens had normal wings and were taken at black light 5.4 and 9.1 mi. E. Cuernavaca in June and July.

*Bionomics.* — Members of this species have been taken from June to November and at altitudes from 4,340 to 6,800 feet. Ball's data indicate *cyanippa* has been taken: at black light in thorn forest with old lava flow substrate 5.4 mi. E. Cuernavaca, 4,600 feet; under cover on damp ground consisting of old lava flow 3.6 mi. E. Cuernavaca, 4,600 feet; at black light on sides of steep canyon with subtropical deciduous, rather open vegetation 9.1 mi. E. Cuernavaca, 4,300 feet; in wet, deep litter on slopes of southwest-facing ravine with bromeliads in oak forest 26.1 mi. S. Tecalitlan, 6,800 feet; and under stones and in litter from few trees near small creek bed at the edge of corn field in vicinity of tropical montane forest 6.5 mi. S. Talpa de Allende, 4,340 feet.

### 9.3 *Notiobia (Anisotarsus) hilariola* (H. W. Bates)

(Figs. 8, 89, 90, 143)

*Anisotarsus hilariolus* H. W. Bates, 1891: 239. [Lectotype (BMNH), here designated, ♂ labeled: "Lectotype", "Omiteme Guerrero 8000 ft. July. H. H. Smith", "Anisotarsus hilariolus Bates". Label added stating: "LECTOTYPE Anisotarsus hilariolus Bates By G. R. Noonan". TYPE LOCALITY: Omiteme, Guerrero, 8,000 ft., Mexico as originally cited].

*Description.* — Body length 10.9 to 11.3 mm.

Color. Dorsum somewhat shiny, especially in ♂; labrum rufopiceous to black, remainder of head dark blue, dark purple, bluish black, or purplish black; pronotum dark blue, dark purple, or greenish purple, coloration more prominent than in head; elytron greenish or aeneous and in some specimens with cupreous tinge (coloration of dorsum best observed

under natural daylight or under equivalent light from fluorescent lamp). Venter and palpi piceous to rufopiceous. Legs rufopiceous, to black. Antenna with first 3 segments piceous to rufopiceous.

Head. Labral apex slightly to moderately emarginate medially. Clypeal apex slightly emarginate medially. Frons with microsculpture of isodiametric mesh, obsolescent medially in ♂. Width of gena and first antennal segment as in *lamprota*. Supra-antennal ridge arcuate, curved first outwards then inwards.

Thorax. Pronotum (Fig. 8) with posterior angle rounded; anterior angle prominent; lateral bead prominent, especially near posterior angle; basal bead complete; microsculpture of isodiametric mesh, obsolescent medially in ♂, not obsolescent medially in ♀ but less prominent medially than laterally. Prosternum with scattered fine short setae elsewhere except medially. Proepimeron with fine short pubescence near front coxae. Mesosternum with fine short pubescence in some specimens. Metasternum with irregular short fine pubescence in region of midcoxae.

Legs. Dorsum of tarsi pubescent.

Elytron. Humerus of some specimens with faint indication of tooth; intervals flat to slightly convex; interval III with setigerous puncture at apical 1/3 or 1/4; subapical sinuation slight to moderate; sutural angle rounded; microsculpture in ♂ of isodiametric mesh and nearly obsolete medially, in ♀ of isodiametric mesh and slightly less prominent medially.

Abdomen. One ♂ from Omiltemi, Guerrero with 2 pairs of ambulatory setae on sternum VI.

Male genitalia. Median lobe (Figs. 89, 90) with apex relatively elongate; sclerotized virga present to left of ostium; large prominent spine, arising from internal sac, visible beneath virga and projecting into ostium.

*Flight*. — The hind wing is vestigial in all specimens examined.

*Bionomics*. — Members of this species have been taken at altitudes from 6,300 to 8,000 feet during July and August. Ball's data indicate *hilariola* has been taken: in leaf litter near temporary ponds in palm-oak-pine forest 13.9 mi. W. Chilpancingo, 6,300 feet; and under stones on damp open ground in area with remains of cloud forest next to intact cloud forest at Omiltemi, 7,300 feet.

*Distribution and material examined* (21 specimens). This species has been taken from only a small area in the vicinity of Chilpancingo and Omiltemi Guerrero (Fig. 143). Its restricted range may in part be explained by its vestigial hindwing.

#### 9.4 *Notiobia (Anisotarsus) schlingeri* NEW SPECIES

(Figs. 4, 75, 76, 141)

Holotype ♂ labeled: "Mex. Jalisco 12.4 mi. s. Tecalitlan 5,300' August 4, 1967", "Ball, T. L. Erwin, R. E. Leech collectors", "Holotype *Notiobia (Anisotarsus) schlingeri* Noonan".

*Description*. — Body length 9.5 mm.

Color. Specimen apparently with external color of mature beetle but slightly teneral as median lobe not completely sclerotized. Dorsum black except rufopiceous near antennal insertion. Venter and legs piceous except following rufopiceous: prosternum, mesosternum, antecoxal piece, forecoxa, foretrochanter, midcoxa, midtrochanter, hindcoxa, posterior margin of midtrochanter, fore- and midtarsi. Palpi infuscated. Antenna with segments I and II rufous, remaining rufopiceous to infuscated.

Head. Labral apex slightly emarginate medially. Clypeal apex moderately emarginate medially. Frons with fovea small, punctiform; microsculpture of isodiametric mesh, slightly

obsolescent medially. Width of narrowest part of gena less than that of widest part of first antennal segment (w. gena/w. of first antennal segment = 0.64 for both sides).

Thorax. Pronotum (Fig. 4) with posterior angle prominent; lateral margins slightly sinuate posteriorly (more evident on right side); lateral bead prominent; basal bead complete; basal fovea as in Fig. 4; microsculpture consisting of transverse, nearly obsolete mesh medially, elsewhere of isodiametric mesh. Prosternum glabrous except for scattered very short hairs near anterior and lateral margins. Mesosternum with few scattered short hairs. Metasternum with scattered setae in region of midcoxa.

Legs. Midtarsus with segments II to IV laterally expanded and spongy pubescent beneath. Dorsum of foretarsus with few short setae. Dorsum of mid- and hindtarsus glabrous.

Elytron. Humerus obtusely angulate, without tooth; interval III with setigerous puncture at apical 1/3; subapical sinuation slight.

Abdomen. Sternum VI with 2 pairs of ambulatory setae.

Genitalia. Median lobe (Figs. 75, 76) not completely hardened; apex short, blunt, bent ventrad distally. Internal sac in repose with large prominent spine visible in dorsum of median lobe.

Allotype. Female. Same locality and collectors as holotype. Body length 9.08 mm. Fore- and midtarsi same color as rest of legs; sternum VI rufotestaceous; microsculpture of frons slightly more prominent; w. gena/w. of first antennal segment = 0.66; small, shallow outer basal fovea present on pronotum; microsculpture of pronotum more prominent medially and not as transversely stretched; fore- and midtarsi not laterally expanded or spongy pubescent beneath; humerus with prominent tooth; apex abdominal tergum VIII angulate; genitalia as in those of other *Anisotarsus* females; otherwise same as holotype.

Paratypes and variation. (all paratypes with same collectors as for holotype unless otherwise noted). One ♂, Mexico, Guerrero, Omiltemi, 7,300' VII. 14-15 1966, Ball-Whitehead; 1 ♂, 2 ♀♀, Mex. Michoacan, 1.1 mi. E. Angahuan, 7,500' nr. Paricutin, August 13, 1967; 1 ♀, Mexico, Michoacan, 1.3 mi. E. Comanja, 6,600' Rte. 15, VII. 30 1966, black light; 1 ♀ Mex. Jalisco, El Rincon, 30.5 mi. N.W. Los Volcanes, 5,400', August 10, 1967; 1 ♀, Mexico, Jalisco, 7.6 mi. S. Mazamitla, 5,700', Rte. 110, VIII. 6 1966, George E. Ball, D. R. Whitehead collectors; 1 ♂ with same data as holotype; 1 ♂, Temascaltepec, Distrito Federal, G. B. Hinton, 1931. The paratypes range in body length from 8.3 to 9.5 mm. The color is the same as in the holotype except that: the piceous areas listed for the holotype are testaceous to rufotestaceous in some specimens; midtarsus of some specimens testaceous to rufotestaceous; and dorsum in some specimens with slight purple tinge. The form of the pronotum is about the same as for the holotype, but the side varies within populations from moderately sinuate to non-sinuate in the posterior half, and the outer basal fovea varies from absent to present as a shallow depression. The microsculpture of the pronotum is slightly different in males and females as outlined in the description of the holotype and allotype. The humeral angle bears a prominent tooth in all females except the one from 7.6 mi. S. Mazamitla (lacks any evidence of tooth) and is without a tooth in all males.

*Deposition of type material.* — The holotype and allotype are deposited at MCZ and the paratypes at CAS, MCZ, and UASM.

*Derivation of name.* — It gives me great pleasure to name this species after Evert Schlinger who has given me constant encouragement and help during this study and during my years as a graduate student.

*Discussion.* — This species is most similar in appearance to *nitidipennis* but is distinguished by its different distribution and by morphological characters given in the key.



*Bionomics.* — Members of *schlingeri* have been taken in July and August, and at altitudes ranging from 5,300 to 7,500 feet. Ball's data indicate they have been found: under stones on loam soil of clay and gravel in open cleared places adjacent to forest intergrading from oak and pine to cloud forest at Omiltemi, 7,300 feet; in oak-pine litter on red-sand-clay soil near top of east side of north-facing ravine forested with oaks and pines 12.4 mi. S. Tecalitlan, 5,300 feet; in a forest of pines with some oaks and ground of volcanic ash 1.1 mi. E. Angahuan, 7,500 feet; under cover in clear area of oak-pine forest in vicinity of old logging camp at El Rincon, 30.5 mi. N.W. Los Volcanes, 5,400 feet; and under debris on reddish predominantly clay soil in open oak pine forest on slopes of ravine 7.6 mi. S. Mazamitla, 5,700 feet.

*Distribution.* — This species is found in central Mexico (Fig. 141).

#### 9.5 *Notiobia (Anisotarsus) nitidipennis* (LeConte)

(Figs. 16, 39, 73, 74, 135)

*Eurytrichus nitidipennis* LeConte, 1848: 388. [Holotype (MCZ), ♂ labeled: orange disc without lettering, "504", "TYPE 5963", "E. nitidipennis Lec.". TYPE LOCALITY: Georgia as originally cited].

*Anisotarsus cephalus* Casey, 1914: 215. [Holotype (USNM), ♀ labeled: "Fla", "Casey bequest 1925", "TYPE USNM 47978", "cephalus Csy.". TYPE LOCALITY: Florida as originally cited. NEW SYNONYMY].

*Anisotarsus delicatus* Casey, 1914: 214. [Lectotype (USNM), designated by Lindroth (1968 and 1969a), ♀ labeled: "NC", "Casey bequest 1925", "TYPE USNM 47977", "delicatus Csy". TYPE LOCALITY: Asheville, North Carolina as originally cited].

*Anisotarsus tenuitarsis* Casey, 1914: 215. [Lectotype (USNM), here designated. ♂ labeled: "Fla", "Casey bequest 1925", "TYPE USNM 47979", "tenuitarsis Csy". Additional label added stating: "LECTOTYPE *Anisotarsus tenuitarsis* Casey By G. R. Noonan". TYPE LOCALITY: Lake Worth, Florida as originally cited. NEW SYNONYMY].

*Harpalus conspectus* Casey, 1924: 103. [Holotype examined and synonymized by Lindroth (1968). TYPE LOCALITY: Mt. Royal, Quebec, Canada].

*Harpalus agitabilis* Casey, 1924: 104. [Holotype (USNM), ♂ examined by G. E. Ball. TYPE LOCALITY: District of Columbia as originally cited. NEW SYNONYMY].

*Description.* — Body length 5.9 to 8.2 mm.

Color. Dorsum dark piceous to black, in most specimens with prominent greenish or aeneous tinge; elytral suture, epipleuron, and margins of labrum and pronotum rufescent or testaceous in most specimens. Venter with apex of abdominal sternum VI rufescent or testaceous in most specimens; remainder piceous to black. Legs testaceous to rufotestaceous. Antenna with first segment testaceous to rufotestaceous, remaining various.

Head. Labral apex slightly to moderately emarginate medially. Clypeal apex slightly to moderately broadly emarginate medially. Frons with fovea obsolescent; microsculpture of isodiametric mesh. Head moderately to relatively large but with eye smaller, less protruding than in related species (Fig. 39). Gena as in *terminata*.

Thorax. Pronotum (Figs. 16, 39) with posterior angle varied from subdentate (Fig. 16) to rounded but prominent (Fig. 39); sides strongly convergent basally, rectilinear or faintly sinuate; lateral depression slightly evident near middle; basal bead complete in most specimens; basal fovea obsolescent; microsculpture of isodiametric mesh with tendency to become obsolete and transversely elongated medially. Prosternum pubescent. Proepisternum with scattered setae anteriorly. Mesosternum sparsely pubescent in some specimens. Metasternum with scattered pubescence.

Legs. As in *terminata*.

Elytron. As in *terminata*.

Abdomen. Sternum VI of ♂ with 1 or 2 pairs of ambulatory setae.

Male genitalia. Median lobe (Figs. 73, 74) with apex short, bluntly to nearly acutely rounded at tip. Internal sac in repose with large slender spine visible in distal region of membranous area of dorsum; everted sac with the large slender spine located proximal to median lobe and with apical field of enlarged scales.

*Variation.* — The shape of the pronotal posterior angle shows a north-south cline. The angle tends to be prominent and projecting (Fig. 16) in specimens from Canada and northern United States and southward becomes progressively more rounded and less prominent.

Intrapopulational variation occurs in: body size and color; degree of emargination of labral and clypeal apices; and shape of apex of female abdominal tergum VIII. The relative size of the head varies somewhat, but I have not seen sufficiently large series from individual localities to determine whether this variation is inter- or intrapopulational.

*Discussion.* — The form *cephalus* was characterized by Casey (1914), who listed *nitidipennis* as a species not seen, as having a relatively large head. Van Emden (1953) apparently never saw the types of *cephalus* or *nitidipennis* and separated *cephalus* from *nitidipennis* by this character. Lindroth (1968) expressed doubt about the validity of *cephalus* as a separate species. Actually, the head varies from moderately to relatively large in *nitidipennis*, and the holotype of *cephalus* is clearly a member of this species. The form *delicatus* was also described by Casey in 1914 who as mentioned above was not familiar with *nitidipennis*. Van Emden (1953) and Lindroth (1968) treated it as conspecific with *nitidipennis*, and the lectotype and 5 paralectotypes are clearly members of *nitidipennis*. Casey (1914) also described *tenuitarsis* without being familiar with *nitidipennis*. Van Emden (1953) correctly treated *tenuitarsis* as conspecific with *cephalus*. *Harpalus agitabilis* was proposed by Casey (1924) on the basis of a single male holotype; G. E. Ball (personal communication) has examined this male holotype and found it conspecific with *nitidipennis*.

*Flight.* — Leng (1915) reported members of this species taken at light at Fort Myers, Florida on March 30 and April 22 and as common at light in Mobile Co., Alabama. Lindroth (1968) mentioned specimens appeared in great number among drift material on the shore of Lake Erie at Long Point, Ontario, Canada.

*Bionomics.* — I have seen specimens collected from February into November, and Blatchley (1910) reported specimens taken from April 9 to December 25 in Indiana. Blatchley also reported specimens as occurring beneath cover in sandy localities in Indiana. Leng (1915) cited specimens taken at Everglade, Florida in a grassy meadow with low bushes. Lindroth (1968) stated that Larson found specimens "on clearings with moss but little higher vegetation" in Quebec, Canada.

*Distribution and material examined* (142 specimens). I have seen specimens from southern Canada south into Florida and southwest into Texas (Fig. 135). Blatchley (1910) reported this species as being found in Indiana "Throughout the western half of State; frequent in the southern counties, rare northward." Van Emden (1953) reported seeing a single specimen labeled as being from Colorado. Lindroth (1968) and Leng (1915) reported specimens from several localities in Canada and Florida respectively, and these localities were used in constructing Fig. 135.

9.6 *Notiobia (Anisotarsus) maculicornis* (Chaudoir)

(Figs. 9, 83, 84, 134)

*Harpalus maculicornis* Chaudoir, 1843: 787. [Lectotype (MNHP), here designated, ♂ labeled: "New Orleans", "Ex Musaeo Chaudoir". Additional label added stating: "LECTOTYPE *Harpalus maculicornis* Chaudoir By G. R. Noonan". TYPE LOCALITY: New Orleans, Louisiana as originally cited].

*Harpalus patronus* Casey, 1914: 89. [Holotype (USNM), ♀ examined by G. E. Ball. TYPE LOCALITY: Morgan City, Louisiana, as originally cited. NEW SYNONYMY].

*Anisodactylus depressus* Notman, 1919: 236. [Lectotype (USNM), here designated, ♂ labeled: "Austin 10/20 Texas", "*Anisodactylus depressus* TYPE". Additional label added stating: "LECTOTYPE *Anisotarsus depressus* Notman By G. R. Noonan". TYPE LOCALITY: Austin, Texas as originally cited. NEW SYNONYMY].

*Description.* — Body length 12.7 to 13.1 mm.

Color. Dorsum and venter black to piceous. Legs and palpi rufopiceous to black. Antenna with segment I rufous; segment II rufous in most specimens, rufopiceous to piceous in some specimens; segment III piceous except in some specimens with rufous apex; segment IV testaceous to piceous; remaining segments in most specimens rufotestaceous except for median longitudinal black bar.

Head. Labral apex prominently emarginate medially. Clypeal apex broadly emarginate medially and in many specimens exposing base of labrum. Remainder as in *terminata*.

Thorax. Pronotum (Fig. 9) with posterior angle prominent, nearly right; lateral depression obsolete to prominent, wider and shallower basally; basal bead complete; basal fovea various, with punctures in most specimens; microsculpture of isodiametric mesh with slight tendency to become transversely elongated medially. Venter as in *terminata*.

Legs. As in *terminata*.

Elytron. Humerus somewhat angulate and in most specimens with vestigial tooth; intervals flat to slightly convex; punctuation of intervals as in *terminata* except interval IV may have several non-setigerous punctures; subapical sinuation moderate; sutural angle rounded; microsculpture of isodiametric mesh, slightly granulate in some ♀♀.

Abdomen. Venter as in *terminata*.

Male genitalia. Median lobe (Figs. 83, 84) with apex short, obtusely to acutely rounded at tip, in some specimens slightly removed to the right. Internal sac in repose with prominent spine visible through membranous area of dorsum of median lobe; everted sac with the large spine proximal to ostium and with distal field of small spines.

*Discussion.* — Notman proposed *depressus* as a new species of the genus *Anisodactylus*, and this form has apparently never been re-examined until now. The lectotype and single paralectotype are clearly members of the subgenus *Anisotarsus* and of the species *maculicornis*. *Harpalus patronus* was proposed by Casey (1914) on the basis of a single female holotype. G. E. Ball (personal communication) examined this female holotype and found it conspecific with *maculicornis*.

*Flight.* — Members of this species have been taken at light in a number of localities in Texas and Louisiana and seem to be ready fliers.

*Bionomics.* — Members of this species apparently are active throughout the year. Specimens have been taken on the docks at New Orleans.

*Distribution and material examined* (60 specimens). The species *maculicornis* is found in Texas and Oklahoma east of the 100th meridian and in Louisiana, Arkansas, and eastern Kansas (locality in Kansas not specified) (Fig. 134). I have also seen 1 male labeled as from Orient, Long Island, New York and 1 male labeled as from Riverhead,

Long Island, New York. Since these are the only 2 specimens recorded from Long Island, and this locality is far north of the established range of *maculicornis*, these 2 specimens may have been mislabeled.

9.7 *Notiobia (Anisotarsus) virescens* (Dejean)  
(Figs. 2, 69, 70, 142)

*Harpalus virescens* Dejean, 1831: 839. [Holotype (MNHP), ♂ labeled: "♂", "virescens. m in Mexico.", "Harpalus", "Höpfner", "Ex Musaeo Chaudoir", "Bates vidit 1881". TYPE LOCALITY: Mexico originally cited, here restricted to 5.4 mi. E. Cuernavaca, 4,600', Morelos, Mexico].

*Anisotarsus chloroderus* H. W. Bates, 1882: 50. [Lectotype (BMNH), here designated, ♂ labeled: "Type H. T.", "Puebla", "Mexico Salle Coll.", "B.C.A. Col. I. 1. Anisotarsus chloroderus Bates", "Anisotarsus chloroderus Bates ♂". Additional labels added stating: "Lectotype" and "LECTOTYPE Anisotarsus chloroderus Bates By G. R. Noonan". TYPE LOCALITY: Puebla and Cuernavaca originally cited, here restricted to Puebla, Puebla, Mexico].

*Description.* — Body length 7.7 to 10.4 mm.

Color. Dorsum green, blue, purple, cupreous, or bluish-purple; head, pronotum, and elytron of different colors in some specimens. Venter rufopiceous to piceous. Appendages rufous to piceous.

Head. As in *terminata*.

Thorax. Pronotum (Fig. 2) with posterior angle prominent but rounded; anterior angle obsolescent; lateral depression obsolescent; lateral bead fine apically; basal bead complete in most specimens; basal fovea shallow, not sharply defined, in most specimens somewhat oval in shape, separated from basal angle by convexity; microsculpture of prominent isodiametric mesh. Venter as in *terminata*.

Legs. As in *terminata*.

Elytron. Humerus in some specimens with vestigial tooth; remainder as in *terminata* except microsculpture of isodiametric granulate mesh.

Abdomen. Venter as in *terminata*.

Male genitalia. Median lobe (Figs. 69, 70) relatively narrow; apex short, bluntly rounded, not bent ventrad. Internal sac in repose with large prominent spine visible through membranous area of dorsum of median lobe; everted sac with the prominent large spine located proximal to median lobe and surface of sac with irregular varied distal field of scale-like spines and scales.

*Variation.* — Intrapopulational variation occurs in: body size and color; emargination of labral and clypeal apices; pubescence of prosternum and mesosternum; arrangement of scales and scale-like spines on internal sac.

*Discussion.* — Bates (1882) himself mentioned that he had doubts of *chloroderus* being distinct from *virescens*, and van Emden (1953) treated *chloroderus* as conspecific with *virescens*. The lectotype and 2 paralectotypes of *chloroderus* are clearly members of the species *virescens*.

*Flight.* — George Ball and D. R. Whitehead took 55 males and 28 females at black light 5.4 mi. E. Cuernavaca, and 1 male at light at Colima, Rte. 110. Members of the species are ready fliers.

*Bionomics.* — Members of this species have been collected in central and southern Mexico from June to September at altitudes ranging from 4,300 to 8,000 feet. Ball's data indicate *virescens* has been taken at black light 5.4 mi. E. Cuernavaca, 4,600 feet, in thorn forest on

old lava flow with substrated humus rich soil and outcropping volcanic rock.

*Distribution and material examined* (114 specimens). This species is found in central and southern Mexico (Fig. 142).

9.8 *Notiobia (Anisotarsus) picea* (LeConte)  
(Figs. 7, 81, 82, 133)

*Eurytrichus piceus* LeConte, 1848: 388. [Holotype (MCZ), ♂ labeled: orange disc, "piceus 2" (see discussion of this holotype under notes). TYPE LOCALITY: NovEboraci originally cited, refers to New York (whether city or state not certain)].

*Anisodactylus sayi* Blatchley, 1910: 198. [Nomen novum for *piceus* LeConte, nec Menetries 1844].

*Description.* — Body length 8.1 to 11.3 mm.

Color. Dorsum rufopiceous to piceous, labrum in some specimens lighter than remainder. Venter rufous to rufopiceous. Legs, palpi, and antenna testaceous to rufotestaceous.

Head. Labral apex slightly emarginate medially. Clypeal apex slightly to moderately emarginate medially. Remainder as in *terminata*.

Thorax. Pronotum (Fig. 7) with posterior angle right; lateral depression prominent in most specimens but obsolescent in some; basal bead complete in most specimens; microsculpture obsolete medially, elsewhere of isodiametric mesh. Prosternum with varied fine short pubescence. Proepisternum of some specimens with few fine short setae on anterior portion. Mesosternum with sparse fine pubescence. Metasternum with setae in region of midcoxa.

Legs. Fore- and midtarsi of ♂ as in *terminata*. Dorsum of fore- and midtarsi sparsely pubescent. Dorsum of hindtarsus glabrous in most specimens.

Elytron. Humerus with slight tooth; intervals flat to slightly convex, with or without micropunctures; punctures of interval III as in *terminata*; subapical situation moderate.

Male genitalia. Median lobe (Figs. 81, 82) with apex short and tip rounded (dorsal view) in most specimens as in Fig. 81 but more angulate in some. Internal sac in repose with medium to large sized spine visible in region of ostium; everted sac with the spine located proximal to median lobe and with surface of sac bearing distal field of scale-like spines.

*Discussion.* — The LeConte collection at MCZ contains 1 male and 3 female specimens of *picea*. The first specimen is a female labeled: orange disc, "505", "Type 5962", "*Eurytrichus piceus* Lec.". It cannot be a type specimen since LeConte stated the original description was based on a single male. The second specimen is a male which fits the original description and must be the holotype since it is the only male in the series.

The name *sayi* was proposed by Blatchley (1910) as a replacement for *picea* LeConte which was temporarily preoccupied by *piceus* Menetries when the genus *Dicheirus* was regarded as a subgroup of *Anisodactylus* and *picea* LeConte by Blatchley as a member of *Anisodactylus*. It is now well established (Lindroth, 1968; Noonan 1968) that *piceus* Menetries belongs to *Dicheirus*, a valid separate genus, and that *picea* LeConte belongs in *Anisotarsus* (Lindroth, 1968).

*Flight.* — I have seen specimens taken at light from Pokagon State Park, 7 mi. N. Angola, Indiana; Ann Arbor, Michigan; and Houston, Texas. Lindroth (1968) reported examining 1 specimen which came to light at Trenton, Ontario.

*Bionomics.* — Members of this species have been collected from January to October but have been taken most frequently in July and August. I have seen one teneral female taken on July 17 in Michigan and several possibly teneral specimens taken during June at various

localities.

Lindroth (1968) reported the following ecological information: "At Belleville, Ont., common on a dry, sandy field; at Cowansville, Queb., in a dry sandpit with *Erigeron canadense*; in both places associated with *terminatus*." A female collected at Mineral Springs, Indiana bears a label stating it was found under shelter at the base of a pine tree in a tamarack swamp, and a female from Mason State Forest, Illinois, bears a label stating "bases of tufts grassland".

*Distribution and material examined* (220 specimens). This species is found from southeastern Canada to southeastern Texas (Fig. 133).

### 9.9 *Notiobia (Anisotarsus) flebilis* (LeConte)

(Figs. 15, 71, 72, 138)

*Eurytrichus flebilis* LeConte, 1863: 16. [Lectotype (MCZ), here designated ♂ labeled: gold disc with no lettering, "flebilis 2." Label added stating: "LECTOTYPE *Eurytrichus flebilis* LeC. By G. R. Noonan". TYPE LOCALITY: Cape San Lucas, Lower California as originally cited].

*Anisotarsus castaneus* Bates, 1884: 270. [Lectotype (BMNH), here designated, ♂ labeled: "Type H. T.", "Presidio, Mexico. Forrer.", "B.C.A. Col. I. 1. *Anisotarsus castaneus*, Bates.", "*Anisotarsus castaneus* Bates". Labels added stating: "Lectotype", and "LECTOTYPE *Anisotarsus castaneus* Bates By G. R. Noonan". TYPE LOCALITY: Presidio, Mexico as originally cited (according to Selander and Vaurie, 1962, refers to Presidio de (or near) Mazatlan, Sinaloa, Mexico. "A Forrer locality presumably referring either to the Rio Presidio or to a village on the river. The railroad crosses the Rio Presidio a few kilometers east of Mazatlan at 23° 10', 106° 14'.") NEW SYNONYMY].

*Description*. — Body length 7.3 to 10.9 mm.

Color. Dorsum and venter dull brown to rufopiceous. Appendages testaceous to rufotestaceous.

Head. As in *terminata*.

Thorax. Pronotum (Fig. 15) with posterior angle prominent but rounded; lateral depression of most specimens evident in region of lateral seta; basal bead complete; basal fovea shallow, in most specimens somewhat circular; outer fovea near posterior angle absent; microsculpture of isodiametric mesh with tendency towards transverse mesh medially. Prosternum completely pubescent or with glabrous median area; Remainder as in *terminata*.

Legs. As in *terminata*.

Elytron. Humerus without tooth; humeral angle obtuse; microsculpture of subgranulate isodiametric mesh; remainder as in *terminata*.

Male genitalia. Median lobe (Figs. 71, 72) with apex short, blunt. Internal sac in repose with elongate prominent spine visible in distal portion of membranous area of dorsum; everted sac with spine located proximal to median lobe, in some specimens with second much smaller medium sized spine located near the large spine, surface of sac with distal field of scales, microspines, and spine-like scales.

*Variation*. — I have not seen sufficient series of specimens from individual localities to be able to determine whether most of the observed variation is intra- or interpopulational. However, variations in body size and pubescence of the prosternum appear to be intrapopulational.

*Discussion*. — Van Emden (1953) incorrectly applied the name "*flebilis castaneus*" to this species, termed a form from California and Arizona "*flebilis flebilis*" and a form found in southern United States and Mexico "*flebilis purpurascens*". However the lectotype of

*flebilis* is conspecific with the lectotype of *castaneus*, and both types are members of a species occurring in Guadalupe Island, southern Baja California, and the Mazatlan region of Mexico. The form found in California and Arizona and called "*flebilis flebilis*" by van Emden is conspecific with the form found in southern United States and Mexico which van Emden called "*flebilis purpurascens*". These two forms thus constitute a valid species, *purpurascens*, separate from true *flebilis*.

The series of *flebilis* in the LeConte collection at MCZ consists of 5 specimens, each bearing a gold disc as the only locality label, and 2 specimens from Guadalupe Island. The first 5 appear to be members of the original type series while the 2 from Guadalupe Island clearly are not. The first specimen of *flebilis* is a female labeled: gold disc without any lettering, "Type 5961", "E. *flebilis* Lec.". (gold disc equals California according to LeConte's color code). Since the median lobe of *flebilis* bears crucial taxonomic characters, I designate the second specimen, a male, as the lectotype.

*Bionomics*. — No information available other than Michelbacher and Ross collected a single female on July 28, 1938 at Mesquital, Lower California.

*Distribution and material examined* (60 specimens). This species has a disjunct distribution being found: on Guadalupe Island; in southern Baja California at Cape San Lucas, Mesquital, between San Jose del Cabo and Triunfo, and at San Jose del Cabo; and at Presidio de Mazatlan, Sinaloa, Mexico (Fig. 138).

#### 9.10 *Notiobia (Anisotarsus) purpurascens* (H. W. Bates)

(Figs. 3, 67, 68, 145)

*Anisotarsus purpurascens* H. W. Bates, 1882: 50. [Lectotype (BMNH), here designated, ♂ labeled: "Las Vigas, Mexico. Hoege", "B.C.A. Col. I. 1. *Anisotarsus purpurascens*, Bates". Labels added stating: "Lectotype", and "LECTOTYPE *Anisotarsus purpurascens* Bates By G. R. Noonan". TYPE LOCALITY: Orizaba and Las Vigas, Mexico originally cited, here restricted to Las Vigas, Veracruz, Mexico].

*Anisotarsus calathoides* Casey, 1914: 212. [Lectotype (USNM), here designated, ♂ labeled: "Ari", "Casey bequest 1925", "Type USNM 47970", "*Calathoides* Csy". Label added stating: "LECTOTYPE *Anisotarsus calathoides* Casey By G. R. Noonan". TYPE LOCALITY: Arizona as originally cited. NEW SYNONYMY].

*Anisotarsus convexulus* Casey, 1914: 210. [Lectotype (USNM), designated by Lindroth (1968 and 1969a), ♀ labeled: "Tex", "Casey bequest 1925", "TYPE USNM 47968", "*convexulus* Csy". TYPE LOCALITY: Galveston, Texas as originally cited. NEW SYNONYMY].

*Anisotarsus extraneus* Casey, 1914: 211. [Holotype (USNM), ♀ labeled: "Los Angeles Co. Cal.", "Casey bequest 1925", "TYPE USNM 47969", "*extraneus* Csy". TYPE LOCALITY: Los Angeles Co., California as originally cited. NEW SYNONYMY].

*Anisotarsus inaudax* Casey, 1914: 211. [Lectotype (USNM), designated by Lindroth (1968 and 1969a), ♀ labeled: "Tex", "Casey bequest 1925", "TYPE USNM 47967". TYPE LOCALITY: Galveston and westward nearly to El Paso originally cited by Casey, restricted to Galveston, Texas by Lindroth (1968). NEW SYNONYMY].

*Description*. — Body length 7.7 to 10.4 mm.

*Color*. Dorsum with labrum same color as remainder of head or somewhat lighter; remainder of head and pronotum rufopiceous to piceous or same color as elytron which may be bluish or purplish black or reddish purple; elytron rarely with faint greenish tinge. Venter rufopiceous to piceous. Appendages testaceous to rufous.

*Head*. As in *terminata*.

Thorax. Pronotum (Fig. 3) with posterior angle prominent but rounded; lateral depression evident in region of lateral seta in most specimens; basal bead complete in most specimens; basal fovea of most specimens consisting of shallow circular or elliptical depression; base of most specimens with outer fovea near posterior angle; microsculpture of isodiametric mesh with slight tendency towards transverse condition medially; shape of base various. Prosternum completely pubescent or with median glabrous area. Remainder of venter as in *terminata*.

Legs. As in *terminata*.

Elytron. Humerus without tooth; humeral angle varied from obtuse to acute; remainder as in *terminata*.

Abdomen. Sternum VI with 1 or 2 pairs of ambulatory setae in ♂.

Male genitalia. Median lobe (Figs. 67, 68) with relatively broad shaft; apex short and in most specimens acutely pointed. Internal sac in repose with large prominent spine visible in distal portion of dorsum of median lobe; everted sac with the large spine located proximal to median lobe and with surface of sac bearing irregular and varied mixture of scale-like spines and scales.

*Variation.* — Intrapopulational variation occurs in: degree of narrowing of basal portion of pronotum; presence or absence of outer fovea on pronotum; shape of basal fovea of pronotum; pubescence of prosternum; and body size.

*Discussion.* — This species was formerly known by the name "*flebilis*". However an examination of the lectotype of *flebilis* showed that it is actually a member of the species which was previously termed "*castaneus*" occurring in Baja California, Guadalupe Island and western Mexico. Since *flebilis* has priority, it must replace the name "*castaneus*", and the species occurring in western and southern United States and Mexico must be renamed with its senior synonym *purpurascens*.

The type series at the BMNH of the species *purpurascens* contains a male from Orizaba, Mexico bearing a type label. This type label apparently was added during routine curating because a lectotype has not previously been designated in publication for *purpurascens*. Since this male is in a state of decay and falling apart, I have decided to designate a male from Las Vigas, Mexico as lectotype.

The relationship of the form *calathoides* to *purpurascens* was not mentioned by Casey (1914) since he did not key out the latter species. However, the male lectotype and the paralectotypes of *calathoides* clearly fit my concept of the species *purpurascens*. Van Emden (1953) and Lindroth (1968) considered *convexus* conspecific with *picea*. However, the median area of the pronotum of the lectotype has prominent microsculpture whereas in *picea* the microsculpture is always obsolete medially. The lectotype and accompanying paralectotypes of *convexus* all agree with the characters described for *purpurascens*. The form *extraneus* was based on a single female from California. Casey's concept of its relationship to *purpurascens* can not be determined since he did not treat *purpurascens* in the key to species and listed *flebilis* (species name at time applied to *purpurascens*) as a species not seen by him. The holotype of *extraneus* agrees completely with my definition of the species *purpurascens*. The form *inaudaux* was treated as conspecific with *picea* by van Emden (1953) and Lindroth (1968). However, its lectotype and paralectotypes cannot be members of that species for the same reasons mentioned concerning *convexus*. Rather they are members of the species *purpurascens*.

*Flight.* — I have examined 1 male and 2 females taken at light on May 7, 1938 at Anaheim, California and 1 male taken at light at San Diego, California on July 9, 1928. On September 2, 1964 I collected a female at black light 18 mi. S.W. Sinaloa, Mexico, and on July 10, 1964 I took a male at black light in Toll Road Public Campground, San



Bernardino Mountains, California. Moore (1937) reported many specimens of *extraneus* (synonym of *purpurascens*) taken at light in Mission Valley, California between August 20 and 25, 1928.

*Bionomics.* — Adults of this species apparently are present throughout the entire year. The species appears on the basis of collection data not to be common at any one locality since only 1 or 2 specimens are usually taken at a single locality and date.

On May 14, 1967 I collected a single female from under a board on the ground in the area of Newport Bay, near Newport, California. The ground beneath the board and within 3 to 4 feet of it consisted of moist clay bare of vegetation and cracked with deep fissures. The spot covered by the board was evidently earlier occupied by a temporary pond. The ground to within 3 to 4 feet of the board was covered with grass. The collecting site had scattered *Salix* sp., was in the bottom of a wash, and evidently received sun during most of the day. Several hours were spent collecting in this area, but no additional specimens were seen. Kenneth Cooper collected one female in a clump of cottonwoods and cattails near the borders of a permanent pond in Whitewater Canyon, (Riverside County) California on January 28, 1968.

Within mainland Mexico, George Ball and his students have taken this form: in litter under trees in canyon with sycamore, walnut, *Acacia*, agave, oaks, *bromeliads*, and Spanish Moss 14.8 mi. W. Linares, Rte. 60, 2,400 feet; under stones on sandy soil near small creek in deep gully 3.2 mi. S. Galeana; under stones on bare, chalky, muddy, abrasive ground near marl pond in area with desert type vegetation 3 mi. W. Galeana, 5,800 feet; under stone on river floodplain some distance from edge of Rio Salinas at Cienega de Flores, 1,200 feet; under cover in abandoned gravel pit near pond 11.7 mi. N. Montemorelos, Rte. 85, 1,550 feet; under cover on wet ground in vicinity of small stream in *Acacia*-grassland 5.3 mi. N. Aguascalientes, 6,100 feet; and under stones and in litter at edge of cornfield bordered by wet pine-oak forest at 33.7 mi. N.W. Los Volcanes, 5,400 feet.

*Distribution and material examined* (207 specimens). This species is found in central and southern California, southern United States and northern Mexico (Fig. 145).

#### 9.11 *Notiobia (Anisotarsus) terminata* (Say), 1823

(Figs. 10, 11, 12, 13, 61, 62, 63, 64, 65, 66, 144)

*Feronia terminata* Say, 1823: 48. [Neotype (MCZ), designated by Lindroth (1969b), ♂ labeled: "Cleveland 7-15-27", "John Gehring Collection", "Neotype *Feronia terminatus* Say design. Lth.", "Anisotarsus terminatus det. Lindroth 68". TYPE LOCALITY: Cleveland, Ohio, as designated by Lindroth (1969b)].

*Harpalus similis* Say, 1823: 29. [Neotype (MCZ), designated by Lindroth (1969b), ♂ labeled: "Fla", "Collection of Frederick Allen Eddy", "Neotype *Harpalus similis* Say design. Lth.", "Anisotarsus similis Say (agilis Dejean) det. Lindroth 68". TYPE LOCALITY: North Carolina as originally designated by Say. NEW SYNONYMY].

*Harpalus agilis* Dejean, 1829: 357. [Lectotype (MNHP), here designated, ♂ labeled: "agilis. m in Amer. Bor", "similis Say.", "Leconte", "Ex Musaeo Chaudoir". Label added stating "LECTOTYPE *Harpalus agilis* Dejean By G. R. Noonan". TYPE LOCALITY: "Amerique septentrionale" originally cited, here restricted to Archbold Biological Station, Highland Co., Florida. NEW SYNONYMY].

*Harpalus ocreatus* Say, 1834: 433. [Neotype (MCZ), here designated, ♂ labeled: "Mex., Chiapas. San Cristobal las Casas 7000' IX. 6. 65", "George E. Ball D. R. Whitehead collectors". Label added stating: "Neotype *Harpalus ocreatus* Say design. G. R. Noonan". (see discussion section for further information). TYPE LOCALITY: Mexico originally

- cited, here restricted to San Cristobal las Casas, Chiapas, Mexico. NEW SYNONYMY].  
*Harpalus testaceus* Haldeman, 1843: 302. [Type not located. TYPE LOCALITY: south-eastern Pennsylvania as originally cited].
- Anisotarsus foveicollis* H. W. Bates, 1884: 269. [Lectotype (BMNH), here designated, ♂ labeled: "Type H. T.", "V. de Chiriqui, 4000-6000 ft. Champion.", "B.C.A. Col. I. 1. Anisotarsus foveicollis, Bates", "Anisotarsus foveicollis Bates ♂". Labels added stating: "Lectotype" and "LECTOTYPE Anisotarsus foveicollis Bates By G. R. Noonan". TYPE LOCALITY: Guatemala, Duenas, and Panama, Volcan de Chiriqui originally cited, here restricted to Volcan de Chiriqui, Chiriqui, Panama. NEW SYNONYMY].
- Anisotarsus floridanus* Casey, 1914: 214. [Lectotype (USNM), here designated, ♂ labeled: "Fla", "♂", "Casey bequest 1925", "TYPE USNM 47982", "floridanus Csy.". TYPE LOCALITY: Florida originally cited, here restricted to Archbold Biological Station, Highland Co., Florida. NEW SYNONYMY].
- Anisotarsus subvirens* Casey, 1914: 213. [Lectotype (USNM), designated by Lindroth (1968 and 1969a), ♀ labeled: "Tex.", "Casey bequest 1925", "TYPE USNM 47976", "subvirens Csy.". TYPE LOCALITY: Austin, Texas as originally cited. NEW SYNONYMY].
- Anisotarsus angusticollis* Casey, 1924: 137. [Lectotype (USNM), designated by Lindroth (1968 and 1969a), ♂ labeled: "Mo.", "♂", "Casey bequest 1925", "TYPE USNM 47975". TYPE LOCALITY: St. Louis, Missouri as originally cited].
- Anisotarsus connivens* Casey, 1924: 139. [Holotype (USNM), ♂ labeled: "Marion County", "♂", "Casey bequest 1925", "TYPE USNM 47981", "connivens Csy.". TYPE LOCALITY: Marion County, Florida as originally cited. NEW SYNONYMY].
- Anisotarsus fuscipennis* Casey, 1924: 137. [Lectotype (USNM), designated by Lindroth (1968 and 1969a), ♂ labeled: "Bayfld, Wis Wickham.", "Casey bequest 1925", "TYPE USNM 47971", "fuscipennis Csy.". TYPE LOCALITY: Bayfield, Wisconsin, and Marquette, Michigan originally cited, restricted to Bayfield, Wisconsin by Lindroth (1968)].
- Anisotarsus hebes* Casey, 1924: 136. [Lectotype (USNM), here designated, ♂ labeled: "Dallas Texas", "♂", "Casey bequest 1925", "TYPE USNM 47974", "hebes Casey". Label added stating: "LECTOTYPE Anisotarsus hebes Casey By G. R. Noonan". TYPE LOCALITY: Dallas, Texas as originally cited. NEW SYNONYMY].
- Anisotarsus innerans* Casey, 1924: 138. [Holotype (USNM), ♂ labeled: "Mo.", "♂", "Casey bequest 1925", "TYPE USNM 47966", "innerans Csy.". TYPE LOCALITY: St. Louis, Missouri as originally cited. NEW SYNONYMY].
- Anisotarsus parallelus* Casey, 1924: 138. [Holotype (USNM) ♀ labeled: "St L Mo", "Casey bequest 1925", "TYPE USNM 47973", "parallelus Csy.". TYPE LOCALITY: St. Louis, Missouri as originally cited. NEW SYNONYMY].
- Anisotarsus subovalis* Casey, 1924: 138. [Holotype (USNM), ♂ labeled: "Charleston Mo", "Casey bequest 1925", "TYPE USNM 47972", "subovalis Csy.". TYPE LOCALITY: Charleston, Missouri as originally cited. NEW SYNONYMY].
- Anisotarsus vernicatus* Casey, 1924: 140. [Holotype (USNM), ♂ labeled: "Everglade Fla Apr. 6. '12", "Casey bequest 1925", "TYPE USNM 47980", "vernicatus Csy.". TYPE LOCALITY: Everglade Co., Florida as originally cited. NEW SYNONYMY].

*Description.* — Body length 6.3 to 9.6 mm.

Color. Dorsum with labrum rufous to piceous, anterior and lateral margins on most specimens lighter than remainder; clypeus rufous to piceous, anterior margin on most specimens lighter; remainder of head rufous to piceous, in some specimens with slight greenish tinge; pronotum rufous to piceous, lateral margin lighter in some specimens, disc in some specimens with slight greenish tinge; elytron rufous to piceous and in most specimens

with evident greenish tinge, in other specimens with faint aeneous tinge or completely lacking tinge. Venter rufous to piceous. Legs and palpi of most specimens testaceous, rufotestaceous in a few specimens. Antenna testaceous to rufous (in a few specimens some or all of the distal 9 segments darker).

Head. Labral apex slightly to moderately emarginate medially. Clypeal apex slightly to moderately emarginate medially. Frons with fovea small, punctiform; microsculpture of isodiametric mesh. Narrowest part of gena narrower than maximum width of first segment of antenna.

Thorax. Pronotum (Figs. 10, 11, 12, 13) with sides slightly to strongly convergent basally; posterior angle prominent; lateral depression various; basal bead present laterally, in some specimens also present medially; outer fovea various; microsculpture of isodiametric mesh with tendency towards transverse mesh medially, in a few specimens nearly obsolete medially. Prosternum with varied pubescence. Proepisternum with scattered fine short setae near anterior margin. Proepimeron with scattered fine short setae near coxa. Mesosternum of some specimens sparsely pubescent. Metasternum irregularly pubescent except medially.

Legs. Midtarsus of ♂ with segments II to IV laterally expanded and spongy pubescent beneath; segment I of many specimens with few adhesive hairs on inner ventral margin. Dorsum of tarsi sparsely pubescent in most specimens.

Elytron. Humerus without tooth; humeral angle of most specimens obtuse but in a few specimens more acute as in *nitidipennis*; intervals flat to slightly convex, with or without micropunctures; interval III with setigerous puncture at apical 1/3 or 1/4; subapical sinuation obsolescent; sutural angle rounded.

Male genitalia. Median lobe (Figs. 61, 62, 63, 64, 65, 66) varied from stout to narrow in form; apex pointed and bent slightly ventrad; internal sac in repose with large prominent spine visible through membranous area of dorsum of median lobe; everted sac with the large prominent spine located proximal to median lobe and with surface bearing varied mixture of scale-like spines and scales.

*Variation.* — This species shows complex geographical and intrapopulational variation. In regards to geographical variation, *terminata* shows a complex pattern of clinal variation. For the purposes of this discussion, 4 “morphs” (which are named and described below) can be recognized. Specimens from localities north of 40 degrees latitude (except for a few places in Nebraska and Iowa which contain members of southern morphs or intergrades with these morphs) are termed members of the “northern morph” and are characterized by: pronotum (Fig. 10) with a wide flattened lateral depression which is translucent and testaceous to rufotestaceous in color, and sides of pronotum only moderately convergent basally; and median lobe relatively stout in form and with internal sac spine located in proximal portion of dorsum when internal sac is in repose (Figs. 61, 62). There is a slight but still evident tendency for the lateral depression of the pronotum to become less pronounced from the north southward towards the 40th parallel. South of the 40th parallel, this reduction in prominence of the lateral depression rapidly becomes more apparent, the sides of the pronotum in specimens from some areas show an increasing tendency to be more strongly constricted basally, the median lobe becomes narrower in form, and the internal sac spine tends to be situated more distally inside the median lobe.

Specimens from south of the 40th parallel can be assigned to 1 of 4 morphs or else regarded as intergrades between these morphs. These 4 morphs are: the “northern morph” situated mainly north of the 40th parallel but with occasional specimens occurring as far south as the 35th parallel; the “Texas morph” centered in Texas; the “Florida morph” centered in Florida; and the “Mexico morph” centered in Mexico.

The Florida morph is characterized by: pronotum lacking lateral depression or at most with only an obsolescent one (Fig. 12); sides of pronotum strongly convergent basally in many specimens; and median lobe relatively slender and with spine of internal sac located distally in most specimens.

The Texas morph is characterized by: pronotum with lateral depression narrow and much less prominent than in specimens of the northern morph (Fig. 11); and median lobe which in most specimens is of the type described for the Florida morph (in some specimens the median lobe may be slightly stouter than in the Florida morph).

The Mexico morph is characterized by: pronotum either lacking lateral depression or having slight to moderate one; and sides of pronotum strongly convergent basally in most specimens. The form of the median lobe varies somewhat within members of this morph, and specimens from northern Mexico have a relatively slender median lobe with a distally located internal sac spine (Figs. 63, 64) as in the Texas and Florida morphs. Southward in Mexico the median lobe tends to become somewhat more stout (Figs. 65, 66) (but apparently never as stout as in the northern morph), and the internal sac spine tends to become more proximally located.

The Texas morph extends north into Kansas, Missouri, Tennessee, Virginia, North Carolina, Nebraska, and Iowa and intergrades in a north-southeastern clinal fashion with the northern morph in this broad area. Southward it intergrades in northern Mexico with members of the Mexican morph. It also intergrades with the Florida morph along the Gulf Coast from Mexico to the Mobile region of Alabama and at scattered localities in Alabama, Georgia, Tennessee, and South Carolina.

The Florida morph occupies all of Florida and extends north into Alabama, Georgia, South Carolina, Tennessee, and Missouri where it intergrades with the northern and Texas morph. This zone of intergradation is broad and there seems to be a visible cline running from north to southeast. The Florida morph also extends west along the Gulf Coast to nearly the Mexican border. From approximately Mobile westward there are found along the Gulf Coast specimens assignable to the Florida or Texas morph and specimens which are clearly intergrades between the 2 morphs. The Texas and Florida morphs thus intergrade over a wide area and seem to be part of a roughly east-west cline.

The Gulf Coast populations of *terminata* grade rapidly into the Mexico morph in northwestern Mexico in regards to pronotal characters. However, as mentioned above, the median lobe of specimens from northern Mexico tends to be similar to that found in the Florida and Texas morphs and changes more slowly than does the pronotum.

The species *terminata* also shows noteworthy intrapopulational variation. In the Texas, Florida, and Mexico morphs, the sides of the pronotum vary within populations from slightly to strongly convergent basally. The following additional characters exhibit intrapopulational variation throughout the species range: body size; color; degree of emargination of the labral and clypeal apices; presence, absence, and prominence of lateral depression of pronotum; presence medially of pronotal basal bead; prominence of pronotal microsculpture; pubescence of venter of body; presence or absence of spongy pubescence on venter of apex of segment I of male midtarsi; number of long setae on posterior margin of hind femur; degree of pubescence of dorsum of tarsi; shape of humeral angle of elytron; shape of elytron; and number and arrangement of scales and scale-like spines on internal sac.

*Discussion.* — In the synonymy of *terminata* I designated a neotype for *Harpalus ocreatus* Say. The insect collection of Say was entirely destroyed after his death except for a few specimens earlier sent to Dejean in France (Lindroth and Freitag, 1969b). I was unable to locate members of *ocreatus* in the Dejean collection. Therefore, in the interest of taxonomic stability it seems best to designate a neotype for *ocreatus*. The selection of the neotype was

based on the original description provided by Say and the concept of the form *ocreatus* followed by subsequent workers. The neotype has been deposited at MCZ as were the Say neotypes previously designated by Lindroth and Freitag (1969b).

The complex variation exhibited by *terminata* has caused several elements to be mistakenly treated as subspecies or species. The form *similis* was treated as a distinct species by van Emden (1953) apparently on the basis of pronotum only slightly narrowed basally and dorsum lacking greenish tinge. The name *agilis* has long been regarded as a synonym of *similis*. The type of *testaceus* has not been definitely located (although Lindroth, 1968, reports the existence of a possible type at MCZ), and previous workers have regarded it as conspecific with *terminata* apparently on the basis of specimens at some time labeled with the name *testaceus*. According to Casey (1924) *angusticollis* is distinguished as narrower and smaller than *terminata*. Van Emden (1953) listed *angusticollis* as possibly conspecific with *terminata*, and Lindroth (1968) correctly treated it as conspecific; its type is merely a small specimen of *terminata*. Another species proposed by Casey in 1924 was *connivens* which was distinguished from *floridanus* (which I regard as conspecific with *terminata*) by: relatively broader hind body or less parallel outline; piceous and not so metallic elytron; and dark rufous prothorax. Casey also proposed the name *fuscipennis* for four specimens which he felt differed from *testaceus* by: being "more abbreviated"; having piceous brown elytron; and having female specimens broader than male ones. The name *hebes* was applied by Casey to three specimens which he regarded as allied to *terminata* but shorter and broader and with relatively shorter and more inflated hind body. Van Emden (1953) tentatively listed *hebes* as a synonym of *terminata subvirens*, and I treat *hebes* as conspecific with *terminata*. The name *parallelus* was used by Casey for a single female supposedly distinguished on the basis of denser and firmer integuments and elytral stria a little courser at the apex. Van Emden treated *parallelus* as conspecific with the species *picea*, but incorrectly since in the pronotum of the holotype of *parallelus* the microsculpture is not obsolete medially; the holotype of *parallelus* possesses the characters given above for *terminata* and is clearly a member of this species. Casey distinguished the form *subovalis* from *terminata* as smaller and having shorter and more oval elytra. Van Emden (1953) listed this form as possibly being conspecific with *terminata*, and the holotype has the characters listed above for *terminata* and is clearly a member of this species. The form *innerans* was cited by Casey as being allied to *agilis* which I regard as conspecific with *terminata*; the male holotype of *innerans* is a specimen somewhat intermediate between the northern and Florida morphs. Casey regarded *verniscatus* as being distinct from *floridanus* (which I regard as a member of *terminata*) on the basis of general body form; the holotype of *verniscatus* is clearly a member of the Florida morph of *terminata*.

Van Emden (1953) recognized 3 subspecies of *terminata* in addition to the nominate one: *subvirens* from Texas and adjacent parts of Oklahoma and Kansas; *ocreatus* from Mexico and Guatemala; and *foevicollis* from Panama and Costa Rica. In addition, he treated as a separate species the form *floridanus* which he reported as occurring in Florida and several southeastern states. The forms *subvirens*, *floridanus* and *ocreatus* correspond respectively to what I term the Texas, Florida, and Mexico morphs. As these morphs are merely segments of clines, they do not warrant separate specific status. I also think they do not warrant formal subspecific status since I believe this formal taxonomic category should be reserved for more distinctly geographically defined entities or preferably not used at all. The form *foevicollis* was distinguished by van Emden from *ocreatus* (the Mexico morph) on the basis of "Average size somewhat smaller, elytra narrower, less rounded at sides, brighter green in male". Van Emden himself admitted that the latter two forms were not very distinct. Body size and color vary within populations of *terminata* as, to a lesser degree, does

the shape of the elytron. I have not been able to find any combination of consistent taxonomic characters for separating specimens from Panama and Costa Rica and more northern locations, and there is no justifiable reason for retaining *foevicollis* as a valid subspecies.

*Flight.* — Specimens of this species have been taken frequently at lights in Canada, United States, and Mexico and are apparently ready fliers.

*Bionomics.* — Members of this species have been collected from March to October in Canada and northern United States and at higher elevations in the southern part of its range. In lowlands of the southeastern United States members have been taken year round. In Mexico specimens have been collected during all months but January and March. This gap may be due to a lack of collecting there during these months.

Lindroth (1968) reports that this species occurs on "dry, open, sandy ground with sparse vegetation, for instance on cultivated land and in gravel pits." Label data reveals that this species has been taken in the United States under a variety of different kinds of debris and stones on the ground.

This species is found in a variety of habitats in mainland Mexico. Summarizing information from Ball's data, *terminata* has been taken on the ground under stones or debris: in open pine, oak, or oak and pine forests; in or near agricultural areas; near water in several habitats; along roadsides; in vegetation near *Carex* marsh in semi-desert area at La Atascosa; in moist areas of high desert country; in cut-over cloud forest of mainly oak and pine with cacti, bromeliads, herbs and grass 21.8 mi. N. Juchatengo, 7,100 feet; and on floodplain with bare, damp, sandy-clay soil about 50 feet from margin of Rio Sabinas Hidalgo, 7.9 mi. E. Sabinas Hidalgo, 800 feet. The various habitats in which *terminata* has been taken in mainland Mexico mostly all have the common feature of being relatively open land without dense forest cover.

It appears that *terminata* feeds at least in part on vegetable material. Blatchley (1910) mentioned that "in September 1903, this species was noted as very common on the heads of the fireweed (*Erechites hieracifolia* L.) in a deadening near Wyandotte Cave, Crawford County, where it was feeding on the seeds." A female at the USNM has pinned into its tray a card stating, "This carabid was reported causing considerable damage to milo seed planted at Lyons, Kansas, Rice Co. June 1945."

Johnson and Cameron (1969) reported interesting data on feeding habits of specimens found on golf courses in New York State. According to them, *terminata* was "A very active grass feeder in laboratory and field." Both sexes of the species ate seeds of the annual blue grass *Poa annua* L. in the laboratory. Gut contents of specimens from the field were composed of predominantly vegetable matter including grass blades, grass seed, and pollen. The species occasionally fed on larvae of *Hyperodes* (Coleoptera:Curculionidae) offered in the laboratory. When given a choice the laboratory specimens fed on "dry seed, seed in fresh panicles, and grass blades in that order." "The gut contents of field-collected specimens taken before mid-June were mostly vegetative portions of grass. . .; after the *P. annua* seed ripened in the field the gut contents were often predominantly seeds."

*Distribution and material examined* (2,665 specimens). The range of this species extends from southeastern Canada, through eastern United States, south along the mountains and highlands of Mexico, and into Central America as far south as Bugaba, Panama (Fig. 144). Four specimens have also been taken from Paget, Bermuda.

#### 9.12 *Notiobia (Anisotarsus) lamprota* (H. W. Bates)

(Figs. 1, 77, 78, 136)

*Anisotarsus lamprotus* H. W. Bates, 1882: 51. [Holotype (BMNH), ♂ labeled: "Type H. T."],

"Veracruz", "Mexico Salle Coll.", "B.C.A. Col. I 1. Anisotarsus lamprotus Bates", "Anisotarsus lamprotus Bates". TYPE LOCALITY: Vera Cruz, Mexico as originally cited].

*Description.* — Body length 10.9 to 12.7 mm.

Color. Dorsum shiny (more so in ♂); head bluish green, bluish purple, less often purplish black; apex and sides of labrum slightly lighter in some specimens than remainder of head; pronotum same color as head but coloration more prominent in some specimens; elytron green, aeneous, or in some specimens cupreous. Venter, legs, palpi, and dorsum of hindtarsus rufopiceous to piceous. Antenna with first three segments at least in part rufopiceous or piceous and remaining segments reddish brown except for median longitudinal dark bar.

Head. Labral apex straight to moderately emarginate medially. Clypeal apex straight to moderately emarginate medially, base of labrum exposed in some specimens. Frons with fovea punctiform and relatively deep, in most specimens with linear medially directed impression; microsculpture of isodiametric mesh, obsolescent medially in some ♂♂. Narrowest part of gena wider than maximum width of first antennal segment. Antenna with relatively elongate segments; segments V to X 1.72 to 2.12 times as long as wide.

Thorax. Pronotum (Fig. 1) with posterior angle prominent; lateral depression present, but very narrow; lateral bead prominent, especially near posterior angle; basal bead complete; microsculpture of isodiametric mesh with tendency to become transverse medially. Prosternum, proepimeron near forecoxa, mesosternum, and metasternum each with short irregular pubescence in some specimens.

Legs. Dorsum of all tarsi sparsely pubescent.

Elytron. Humerus with or without small tooth; intervals flat to slightly convex; intervals III and V of some specimens and interval VII of all specimens with series of apical setigerous punctures; subapical sinuation slight; microsculpture of isodiametric prominent mesh in ♀, in most ♂♂ somewhat obsolescent medially and then appearing medially as fine lines, in some ♂♂ also of weak isodiametric mesh on median portions.

Male genitalia. Median lobe (Figs. 77, 78) relatively stout; apex bent slightly ventrad. Everted internal sac bearing small proximal field of scale-like spines.

*Variation.* — Intrapopulational variation occurs in body size and in pubescence of the venter. One male from 2.5 mi. W. Sontecomapan has an extra pronotal seta (illustrated in Fig. 1) slightly anterior to the usual one.

*Flight.* — George Ball and D. Whitehead collected a male and 3 females at black light 2.5 mi. W. Sontecomapan on June 5 and 20/1966.

*Bionomics.* — This species would seem to be rare, or at least very elusive, where it does occur, and I have not seen more than four specimens from a single locality. Specimens have been taken from May to October at altitudes ranging from 100 to 2,900 feet. Ball's data indicate specimens have been taken in: leaf litter on steep slopes in mountain rain forest containing large trees with buttresses, spiny palms, tree ferns, and vines at El Bastanal, near Coyame, elevation approximately 2,500 feet; among vegetation on rather dry sandy loam in banana-coffee plantation and also in leaf litter in cloud forest at Fortin de las Flores, 2,900 feet; and in moderately deep and wet litter in oak forest 5 mi. N.W. Cautla, 6,600 feet. It appears to be found in mesic, warm or nearly tropical environments.

*Distribution and material examined* (11 specimens). This species has been taken only from the state of Veracruz in Mexico (Fig. 136).

9.13 *Notiobia (Anisotarsus) mexicana* (Dejean)

(Figs. 5, 79, 80, 137)

*Harpalus mexicanus* Dejean, 1829: 288. [Lectotype (MNHP), here designated, ♂ labeled: "mexicanus. Klug in Mexica.", "♂", "Ex Musaeo Chaudoir". Label added stating: "LECTOTYPE *Harpalus mexicanus* Dejean By G. R. Noonan". TYPE LOCALITY: Mexico as originally cited].

*Anisodactylus arizonae* Casey, 1884: 6. [Holotype (USNM), ♂ labeled: "Ari.", "Casey bequest 1925", "TYPE USNM 47964", "arizonae type Casey". TYPE LOCALITY: Arizona as originally cited].

*Stilboldus aztecus* Casey, 1914: 207. [Lectotype (USNM), here designated, ♀ labeled: "Guadalajara, Mexico VIII", "Casey bequest 1925", "aztecus Casey", "TYPE USNM 47965". Label added stating: "LECTOTYPE *Stilboldus aztecus* Casey By G. R. Noonan". TYPE LOCALITY: Guadalajara, Jalisco, Mexico as originally cited].

*Description.* — Body length 9.9 to 13.6 mm.

Color. Dorsum piceous to black, in most specimens with purple or bluish purple tinge, margins of labrum lighter than rest of dorsum in some specimens. Venter and legs rufopiceous to black. Palpi rufopiceous to piceous. Antenna rufous to piceous.

Head. Labral apex moderately emarginate medially. Clypeal apex straight to broadly emarginate medially, base of labrum exposed in some specimens. Frons as in *terminata*. Narrowest part of gena wider than maximum width of first antennal segment. Antenna with distal segments relatively stout, segments V to X 1.6 to 1.3 times as long as wide.

Thorax. Pronotum (Fig. 5) with posterior angle prominent, in most specimens slightly projected; side straight to sinuate before posterior angle; lateral depression obsolescent; lateral bead very prominent, especially near posterior angle; basal bead complete in most specimens; microsculpture of isodiametric mesh, somewhat less prominent medially. Prosternum, anterior part of proepisternum, mesosternum, mesepisternum near juncture with mesosternum, and metasternum in region of midcoxa with fine short pubescence in some specimens.

Legs. Dorsum of tarsi moderately to densely pubescent.

Elytron. Humerus of some specimens with vestigial tooth; intervals flat to slightly convex; intervals II to VII of most specimens with apical series of small setigerous punctures; subapical sinuation slight to obsolescent; sutural angle rounded.

Male genitalia. Median lobe (Figs. 79, 80) relatively stout; apex short, tip bent ventrad. Internal sac without discernible armature.

*Variation.* — Intrapopulation variation occurs in: body size, color and relative stoutness; emargination of labral and clypeal apices; shape of pronotal side before posterior angle; prominence of pronotal posterior angle; presence of pronotal basal bead medially; pubescence of thoracic venter; pubescence of tarsal dorsum; occurrence of vestigial tooth on elytral humerus; convexity of elytral intervals; punctuation of elytral intervals II to VII; and prominence of elytral subapical sinuation.

*Discussion.* — Casey (1884) described *arizonae* as a member of *Anisodactylus* apparently before he was familiar with the genera of Carabidae. In 1914 he treated it as a species of his new genus *Stilboldus* which he regarded as related to *Anisotarsus*. Van Emden (1953) found it indistinguishable from *mexicana* and treated it as conspecific, as did Lindroth (1968); the holotype of *arizonae* is clearly *mexicana*. Casey (1914) distinguished *aztecus* by "much stouter in build and larger in size", but van Emden noted variation in body size and stoutness in Mexico, Guatemala, and Costa Rica. Body stoutness and size exhibit intrapopulation variation throughout the entire range of *mexicana*, and the lectotype of



*aztecus* is merely a large, stout bodied example of this species.

*Flight.* — Members of this species do not appear to be ready fliers. I have examined: 1 female taken at light at Portal, Arizona; 1 female taken at UV light 11.6 mi. N. Ocozocuatla, Mexico; and 1 male, 1 female taken at light in Jacala, Mexico. Since 2 is apparently the largest number of specimens taken at light in a single instance, it is possible that the above specimens crawled to the lights in question.

*Bionomics.* — Members of this species have been collected throughout the year at altitudes from 1,000 to 10,000 feet. Within the United States this species apparently is restricted to forests predominantly of pine, oak, and perhaps walnut in mountainous areas of Arizona, New Mexico, and Texas. I took 3 males and 3 females from under rocks on a grassy hillside with scattered oaks at a location 4.8 mi. W. Portal, Arizona. On September 7, 1964, I collected 11 males and 6 females at Bog Springs Public Campground, Madera Canyon, Arizona. The time of collecting was approximately 1:00 a.m., and the specimens were observed crawling over the ground. The area containing the specimens was heavily shaded by oak trees.

Elbert Sleeper has provided me with information concerning the vegetation in the La Laguna area of Baja California, and it is clear from this information that the species occurs there in the Lagunan Woodland as defined by Axelrod (1958).

Within mainland Mexico the species *mexicana* occurs in a wide variety of habitats. Ball's data indicate it has been taken on the ground under debris or rocks: in forests of pine, oak, oak and pine, sycamore and walnut, and thorn; in or along edges of agricultural areas such as sugar cane and corn fields; along roadsides; by water in some habitats; and in moist areas with desert or semi-desert vegetation. It has also been taken under cover in gallery forest of *Celtis* trees 23.8 mi. N.E. Jacala, 5,100 feet.

*Distribution and material examined* (1,083 specimens). This species is primarily centered in highland areas of mainland Mexico but extends into mountainous areas of Arizona, New Mexico, Texas, south to Panama and occurs in the Laguna Mountains of Baja California (Fig. 137).

#### 10 subgenus *Notiobia* Perty

*Notiobia* Perty, 1830: 13. [TYPE SPECIES: *Notiobia nebrionides* Perty, 1830, by monotypy].

*Ragodactylus* Chaudoir, 1835: 431. [TYPE SPECIES: *Rhagodactylus brasiliensis* Chaudoir, 1835, by monotypy].

*Batrachion* Chevrolat, 1842: 500. [TYPE SPECIES: *Notiobia limbipennis*, here designated].

*Batrachium* Agassiz, 1846: 44. [emendation of *Batrachion*].

*Description.* — Body length 7.2 to 13.8 mm.

Color. Various.

Head. Frons with moderate to prominent fovea bearing in most specimens a clypeo-ocular prolongation. Eye of most species large and protruding. Width of narrowest part of gena less than maximum width of first antennal segment. Supra-antennal ridges slightly to strongly divergent anteriorly.

Thorax. Pronotum cordate and with base lobed in most species. Venter, unless otherwise stated, glabrous except for setae at apex of prosternal lobe.

Legs. Fore- and midtarsi of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Hindfemur with 2 long setae on posterior margin unless otherwise mentioned.

Elytron. Interval III with setigerous puncture in apical 1/3; interval VII with small

setigerous subocellate puncture near apex and slightly more proximal ocellate setigerous puncture.

Abdomen. Sternum VI of ♂ with 1 pair of ambulatory setae.

*Discussion.* — *Rhagodactylus* was proposed by Chaudoir (1835) for a single species, *brasiliensis* Chaudoir, 1835. This form was treated as conspecific with *nebrioides*, the type species of *Notiobia*, by Csiki (1932) apparently on the advice of Schauburger.

Dejean (1837, p. 50) listed *Batrachion* as a genus and cited 3 included species, *rana*, *rufipalpus*, and *chalconatum* as members of it. The genus name and the first two species names were apparently supplied by Chevrolat while *chalconatum* was proposed by Dejean. A description or indication was not provided for any of the 4 names cited by Dejean, and consequently his work has no nomenclatural status.

Chevrolat (1842: 500) mentioned Dejean's listing of *Batrachion* and the 3 species names and provided a description of the genus, but he did not provide a description or indication for any of the 3 species. Chevrolat is clearly the author of *Batrachion*. Csiki (1932) listed *Batrachion* as congeneric with *Notiobia*. Until now *Batrachion* has had no valid species. The Dejean collection at the MNHP contains 6 specimens labeled with the manuscript name *chalconatum*. These specimens are members of *Notiobia limbipennis*. In the interest of stability, I have designated *limbipennis* in the synonymy of the subgenus *Notiobia* as the type species of *Batrachion*.

The subgenus *Notiobia* has never been revised. Perty (1830), Bates (1882, 1884) and Putzeys (1878) proposed new species while various other workers have proposed (as members of other taxa) species now known to belong in it.

In this paper I have prepared a revision of the Mexican species of the subgenus along with a Central American form, *umbrifera*, which is closely related to *unbrata* found in Mexico. The named forms not revised by me are: *aeneola* Putzeys, 1878 \*, described from Colombia; *aulica* (Dejean), 1829, seen by me from Bolivia and Brazil; *championi* H. W. Bates, 1882, described on basis of single female from Volcan de Chiriqui, Panama, holotype seen and probably conspecific with *jucunda* Putzeys; *chiriquensis* H. W. Bates, 1884, type series seen from Volcan de Chiriqui, Panama; *concolor* Putzeys, 1878, seen from Colombia, Ecuador, Panama; *disparilis* H. W. Bates, 1878, seen from Nicaragua, Panama, and "Amazonas" which refers to one of 3 regions in Colombia, Peru, or northern Brazil; *dubia* Putzeys, 1878 \*, recorded from Colombia; *incerta* H. W. Bates, 1882, seen from Costa Rica, Nicaragua, Panama; *jucunda* Putzeys, 1878, seen from Costa Rica, Colombia, Ecuador, and Peru; *longipennis* Putzeys, 1878, seen from Dominica, described from Colombia; *nebrioides* Perty, 1830, described from Brazil; *praeclara* Putzeys, 1878 \*, described from Colombia; *ruficrura* (Brullé), 1838, saw type from Bolivia; *similis* Putzeys, 1878 \*, described from Colombia; *transversicollis* Putzeys, 1878 \*, described from Colombia; *viridula* (Dejean), 1829 \*, transferred under name of *viridellus* Csiki, 1832: 1185, nom. nov. from *Harpalus* to *Notiobia* by van Emden (1953: 516), (*viridellus* proposed as replacement for *viridulus* (Dejean) which was preoccupied by *Harpalus viridulus* Fourcroy, 1785 but with transfer to *Notiobia* is no longer preoccupied) described on basis of single specimen from Brazil; and *wilkensi* (Chaudoir), 1837, transferred from *Harpalus* to *Notiobia* by van Emden (1953: 516), have seen specimens labeled as *wilkensi* from Central America and South America. According to unpublished notes of van Emden in BMNH *wilkensi* includes the following named subspecies, *pallipes* Bates, *concolor* Putzeys, *flavicincta* (Erichson), 1847 (tentatively transferred from *Anisotarsus* to *Notiobia* by van Emden, (1953: 520), and *subaurata* Bates (a variety of *pallipes* Bates). Further work is needed to verify the above conclusions. The form *concinna* (Erichson), 1847, was stated by van Emden (1953: 520) to probably belong in *Notiobia* rather than *Anisotarsus*; it will have to be listed as *incertae sedis* until the type is seen.

**Key to the Mexican and one Central American species of the Subgenus *Notiobia****Notes concerning the key.*

The more difficult to understand characters used in the key are discussed here.

The color of body parts has been used in several couplets. Generally the color of a body part on a given specimen is easy to determine and is fairly stable even when examined under different lighting conditions. However, quite often a given structure may have a metallic reflection or tinge in addition to its basic color. This tinge is frequently affected by the type of light used to illuminate the structure. The degree of change produced in the tinge varies from species to species and from one body part to another. The most commonly noted variation in tinge is that when specimens are illuminated by an incandescent lamp and examined under the microscope the normal tinge is frequently not visible, and only the basic color is discernible. The tinges described in couplet 3 are best examined by using daylight or fluorescent lights giving illumination equivalent to daylight. A microscope need not be used in determining tinges described in couplet 3 since they cover relatively large portions of the beetle's dorsum. Specimens keying out to couplet 6 should first be examined under natural or equivalent light without the aid of a microscope. Then if their elytron does not show a greenish, bluish green, or aeneous tinge, they should be examined under a microscope to determine if the elytron is covered only in part with such a tinge. I have found that in specimens with the elytron only partly covered with such a tinge the tinge is visible even when an incandescent lamp is used for illumination. Similarly, specimens keying to couplet 15 are best examined under the microscope, and a normal incandescent lamp may be used.

Body size is mentioned in several couplets and in each instance has been measured as described in the section on measurements.

The length of the scutellar stria in relation to total elytral length is used to separate species in couplet 8. These lengths are measured as follows: length of scutellar stria along the dorsum from origin at an ocellate puncture near base of stria II to apical end; length of elytron along dorsum from apical tip of scutellum to apex of suture.

The presence or absence and prominence of a clypeo-ocular prolongation to the frontal fovea of the head are useful in separating several species. The clypeo-ocular prolongation is present in *obscura* but does not reach the eye and is often difficult to discern. Therefore, a few individuals of *obscura* may key to couplet 2 where they can be separated by re-examining the frontal fovea and noting the other characters given there.

In several species the internal sac of the male median lobe bears a large prominent elongate spine. When the internal sac is in repose inside the median lobe, this spine is found lying beneath the surface of the dorsal membranous area of the median lobe. In order to observe this spine, it is usually necessary that the median lobe be completely wetted with water. Also in some instances it is necessary to clear the median lobe by immersing it for 1 to 2 minutes in a hot solution of 5 to 10 percent potassium hydroxide.

*Key to Mexican and One Central American Species of the Subgenus *Notiobia**

- |       |  |   |
|-------|--|---|
| 1     | Frontal fovea of head bearing clypeo-ocular prolongation which reaches eye in most specimens .....   | 4 |
| —     | Frontal fovea of head punctiform, lacking evident clypeo-ocular prolongation .....   | 2 |
| 2 (1) | Frontal fovea of head actually with faint short clypeo-ocular prolongation (may be difficult to discern); body length 7.2 to 9.5 mm; median lobe with prominent elongate spine visible beneath membranous area of dorsum (Fig. 99); apex of abdominal tergum VIII of ♀ rounded (Fig. 59) ..... |   |
|       | ..... (in part) <i>obscura</i> H. W. Bates, p. 332   |   |
| —     | Frontal fovea of head with clypeo-ocular prolongation completely absent; body  |   |

	length 9.9 to 13.8 mm; median lobe without prominent spine (Fig. 91); apex of abdominal tergum VIII of ♀ angulate (Fig. 55) . . . . .	3
3 (2)	Elytral intervals flat near base; AND Pronotum and elytron rufopiceous with slight greenish or aeneous tinge; AND pronotum and elytron always with same color or tinge . . . . .	<i>leiroides</i> H. W. Bates, p. 327
—	Elytral intervals convex near base; AND pronotum and elytron of all Mexican and some Central American specimens purple or bluish purple; AND pronotum and elytron of differing colors in most Central American specimens, in a few specimens both pronotum and elytron bright bluish green . . . . .	(in part) <i>parilis</i> H. W. Bates, p. 334
4 (1)	Elytron with subapical sinuation prominent (especially in ♀); with spine at suture apex in many specimens (Figs. 47, 48) . . . . .	5
—	Elytron with subapical sinuation moderate to obsolescent (Figs. 49, 50); without spine at suture apex . . . . .	6
5 (4)	Body length 9.3 to 12.0 mm; apex of abdominal sternum VI of ♀ produced into ventrally projected spine (Fig. 131); median lobe with short apex (Figs. 95, 96) . . . . .	<i>limbipennis</i> H. W. Bates, p. 329
—	Body length 7.3 to 8.4 mm; apex of abdominal sternum VI of ♀ unmodified; median lobe with elongate tapered apex (Figs. 97, 98) . . . . .	(in part) <i>umbrifera</i> H. W. Bates, p. 336
6 (4)	Elytron partly or wholly covered with greenish, bluish green, aeneous or cupreous tinge . . . . .	11
—	Elytron rufopiceous to black (if piceous to black then elytron may have purplish or bluish tinge) . . . . .	7
7 (6)	Pronotum with posterior angle rounded and side straight before it (Fig. 22); labral apex prominently emarginate medially (Fig. 57); apex of median lobe moderately long and with tip bent ventrad (Figs. 107, 108) . . . . .	<i>ewarti</i> new species, p. 326
—	Pronotum with posterior angle not rounded, subdentate in most specimens, side straight or sinuate before it (Figs. 18, 20, 24, 25); labral apex at most moderately emarginate medially (Fig. 51); median lobe as in Figs. 91, 92, 93, 94, 99, 100, 105, 106) . . . . .	8
8 (7)	Scutellar stria of elytron very long, length scutellar stria/length elytron always greater than 0.3; median lobe with apex short, blunt, and lacking prominent internal sac spine (Fig. 105); body length 8.4 to 9.7 mm. . . . .	(in part) <i>umbrata</i> H. W. Bates, p. 335
—	Scutellar stria of elytron of normal length, length scutellar stria/length elytron less than 0.2; median lobe with more tapered apex of moderate length and with prominent elongate spine beneath distal portion of dorsal membranous area (Figs. 93, 99) or median lobe lacking prominent spine beneath distal portion of dorsal membranous area (Fig. 91) and body length 11.3 to 13.1mm. . . . .	9
9 (8)	Median lobe without prominent elongate spine beneath distal portion of dorsal membranous area (Fig. 91); body length 11.3 to 13.1 mm; clypeo-ocular prolongation of frontal fovea of head not prominent . . . . .	(in part) <i>parilis</i> H. W. Bates, p. 334
—	Median lobe with prominent elongate spine beneath distal portion of dorsal membranous area (Figs. 93, 99); body length 7.2 to 10.9 mm; clypeo-ocular prolongation of frontal fovea of head various . . . . .	10
10 (9)	Frontal fovea of head with prominent clypeo-ocular prolongation which reaches	

- eye; AND/OR pronotum (Fig. 20) with wide lateral bead and prominent outward projected posterior angle ..... *melaena* H. W. Bates, p. 331
- Frontal fovea of head with faint clypeo-ocular prolongation which does not reach eye; AND/OR pronotum (Fig. 24) with lateral bead less wide and posterior angle not as prominent ..... (in part) *obscura* H. W. Bates, p. 332
- 11 (6) Pronotal posterior angle rounded and pronotal side curved towards posterior angle or rectilinear, not sinuate before posterior angle (Fig. 19) (doubtful instances treated in both couplets) ..... 12
- Pronotal posterior angle not rounded, subdentate in most specimens and pronotal side sinuate before posterior angle in many specimens (Figs. 18, 21, 23, 24, 25) ..... 13
- 12 (11) Hindfemur testaceous; median lobe constricted near apex in dorsal view (Fig. 101) ..... (in part) *pallipes* H. W. Bates, p. 333
- Hindfemur piceous, less often rufopiceous; median lobe not constricted near apex (Fig. 103) ..... *cooperi* new species, p. 325
- 13 (11) Dorsum of hindtarsus piceous to black; body length 11.3 to 13.1 mm. .... (in part) *parilis* H. W. Bates, p. 334
- Dorsum of hindtarsus testaceous to rufotestaceous; body length 7.2 to 9.7 mm. .... 14
- 14 (13) Frontal fovea of head with faint short clypeo-ocular prolongation which does not reach eye; median lobe as in Fig. 99, 100 ..... (in part) *obscura* H. W. Bates, p. 332
- Frontal fovea of head with prominent clypeo-ocular prolongation which reaches eye ..... 15
- 15 (14) Elytron with uniform greenish or cupreous tinge and uniform microsculpture; labral apex strongly emarginate medially ..... (in part) *pallipes* H. W. Bates, p. 333
- Elytron with various shaped greenish or aeneous tinged macula on inner intervals; intervals VI to X near apex always piceous to rufopiceous and with microsculpture more prominent than in macula; labral apex not or only slightly emarginate medially ..... 16
- 16 (15) Elytral macula in ♀ continuous, not divided; apex of abdominal tergum VIII of ♀ angulate (Fig. 54); median lobe with elongate tapered apex (Figs. 97, 98) (Panama and South America) ..... (in part) *umbrifera* H. W. Bates, p. 336
- Elytral macula in ♀ reduced and divided into basal and apical fields; apex of abdominal tergum VIII of ♀ more rounded (Fig. 53); median lobe with short apex (Figs. 105, 106) (Mexico, Guatemala) ..... (in part) *umbrata* H. W. Bates, p. 335

### 10.1 *Notiobia* (*N.*) *cooperi* NEW SPECIES

(Figs. 19, 58, 103, 104, 150)

Holotype. Male. Mexico, Nayarit, Tepic, VII-1-61, Collr: A. E. Michelbacher.

Description. — Body length 10.6 mm.

Color. Dorsum with labrum piceous; remainder of head and pronotum piceous with bluish tinge; elytron bluish green. Venter rufopiceous. Fore- and midlegs with coxae and trochanters rufotestaceous to rufous, remainder rufopiceous. Hindleg with trochanter rufous; coxa, femur, tibia rufopiceous; tarsus blackish; palpi rufopiceous. Antenna with first 3 segments infuscated medially, apices rufopiceous.

Head. Labral apex moderately emarginate medially. Clypeal apex broadly emarginate medially. Frons with fovea punctiform, bearing prominent clypeo-ocular prolongation to eye; microsculpture of isodiametric mesh; supra-antennal ridges only slightly divergent anteriorly.

Thorax. Pronotum (Fig. 19) with side evenly rounded to posterior angle; posterior angle slightly rounded; lateral depression shallow, becoming obsolete posteriorly and merging into area of basal fovea; lateral bead becoming very narrow anteriorly; basal bead complete; basal fovea indistinct, merged with lateral depression; microsculpture of isodiametric mesh, slightly transversely stretched medially. Pro- and mesosterna with few scattered short fine setae.

Legs. Foretibia with 4 spines on outer distal angle. Fore- and midtarsi with dorsum bearing scattered setae on segments I to IV and glabrous on segment V. Hindtarsus with dorsum glabrous.

Elytron. Intervals slightly convex; subapical sinuation slight; sutural angle broadly rounded; microsculpture of isodiametric mesh.

Genitalia. Median lobe (Figs. 103, 104) with apex obtusely rounded and tip bent ventrad. Inverted internal sac with elongate spine visible near distal end of median lobe membranous dorsal area.

Allotype. Female. Same label data as holotype. Body length 11.6 mm. Bluish tinge on dorsum of head and pronotum very slight; elytron piceous, with bluish green tinge which is less pronounced than in holotype. Labral apex slightly emarginate medially. Thorax with mesosternum bearing few scattered setae. Foretibia with outer distal angle bearing 5 spines. Fore- and midtarsus without laterally dilated segments. Dorsum of segments I to IV of foretarsus with scattered setae; dorsum of segment V of foretarsus and of all segments of mid- and hindtarsus glabrous. Elytron with microsculpture of granulate isodiametric mesh. Sternum VI of abdomen with 4 ambulatory setae. Abdominal tergum VIII with broadly rounded apex (Fig. 58). Remainder as in holotype.

Paratypes and variation. (all paratypes bear same label data as holotype). Four males, 3 females. The paratypes range in body length from 9.61 to 12.2 mm. The prominence of the bluish tinge of the head and pronotum and the bluish green color of the elytron varies from the condition described for the holotype to that in the allotype; however, the prominence is not correlated with sex in the paratypes. The labral apex varies from slightly to moderately emarginate medially. The number of spines on the outer distal angle of the foretibia varies from 3 to 5 and does not seem to be correlated with sex. The lateral dilation and dorsal pubescence of the tarsi in males and females is the same as described for the holotype and allotype respectively. The microsculpture of the elytron is as in holotype for males and as in allotype for females.

*Deposition of type material.* — The holotype and allotype are deposited in the California Academy of Sciences and the paratypes in the California Insect Survey Collection at the University of California, Berkeley.

*Derivation of specific name.* — It gives me great pleasure to name this species after Kenneth Cooper who has very kindly assisted me in this and other studies.

*Distribution.* — This species is known only from Tepic, Mexico (Fig. 150).

#### 10.2 *Notiobia (n.) ewarti* NEW SPECIES

(Figs. 22, 57, 107, 108, 147)

Holotype. Male. Mexico, Veracruz, Coyame, Lake Catemaco, VII-1-10-63, D. R. Whitehead, Blk. It.

*Description.* — Body length 8.75 mm.

Color. Dorsum with labrum and clypeus rufotestaceous; remainder of head piceous with slight greenish tinge; pronotum rufopiceous; elytron piceous on disc, becoming rufopiceous near lateral margin. Venter generally piceous but with localized lighter areas. Legs (except rufopiceous hindcoxa) and palpi testaceous. Antennae testaceous. Holotype appears to be slightly teneral, and coloration may be somewhat darker in mature specimens.

Head. Labral apex prominently emarginate medially (Fig. 57). Clypeal apex broadly emarginate medially. Frons with fovea punctiform, bearing clypeo-ocular prolongation to eye; microsculpture of isodiametric mesh; surface with micropunctures; supra-antennal ridges moderately divergent anteriorly.

Thorax. Pronotum (Fig. 22) with sides arcuate anteriorly, convergent and rectilinear posteriorly; posterior angle rounded; lateral depression moderately prominent, complete, widened posteriorly and embracing area of basal fovea; basal bead complete; apical bead complete, but flattened and very fine medially; basal fovea indistinct, merged with lateral depression; microsculpture of isodiametric mesh, slightly transversely stretched medially; disc with micropunctures.

Legs. Foretibia with 2 spines on outer distal angle. Dorsum of tarsi as in holotype of *cooperi*.

Elytron. Scutellar stria moderately long and nearly reaching stria I; intervals very slightly convex and with micropunctures; subapical sinuation slight; sutural angle broadly rounded; microsculpture of isodiametric mesh, slightly stretched transversely in localized areas.

Genitalia. Median lobe (Figs. 107, 108) with apex elongate and tip curved ventrad. Inverted internal sac with large prominent elongate spine visible beneath membranous area of median lobe near ostium.

Paratype. One male, Mexico, 2 mi. S. Simojovel, Chiapas, VI-9-1969, J. M. Campbell. As in holotype except: body length 10 mm.; pronotum and elytron with slight greenish tinge; venter rufous; legs testaceous, rufotestaceous, or rufous; pronotal apical bead absent medially.

*Deposition of type material.* — The holotype is deposited now at UASM but will later be deposited at MCZ. The paratype is deposited in the Canadian National Collection at Ottawa, Canada.

*Derivation of species name.* — It gives me great pleasure to name this species after William Ewart who gave me considerable assistance while I was a graduate student.

*Flight.* — D. R. Whitehead took the holotype at black light at Lake Catemaco in July.

*Bionomics.* — The holotype was collected on July 1-10, 1963 and the paratype on June 9, 1969.

*Distribution.* — This species is known only from the region of Lake Catemaco, Veracruz, and 2 miles south of Simojovel, Chiapas (Fig. 147).

### 10.3 *Notiobia (N.) leiroides* H. W. Bates

(Figs. 18, 55, 91, 92, 151)

*Notiobia leiroides* H. W. Bates, 1878a: 590. [Holotype (MNHP), ♀ labeled: "Vera Cruz", "Notiobia Leiroides Bates". Additional label added stating: "HOLOTYPE Notiobia leiroides Bates Det. G. Noonan 1970". TYPE LOCALITY: Veracruz, Veracruz, Mexico as originally cited].

*Description.* — Body length 9.9 to 13.8 mm.

Color. Dorsum with labrum and in some specimens anterior part of clypeus rufous, remainder rufopiceous and with greenish or brassy tinge. Venter rufopiceous to piceous. Legs

and palpi testaceous to rufopiceous. Antenna testaceous to rufopiceous; one or more of first 3 segments lighter than more distal ones in some specimens.

Head. Labral apex slightly or not at all emarginate. Clypeus with apex emarginate and in some specimens base of labrum exposed; surface wrinkled near apex in most specimens. Frons with fovea punctiform, lacking clypeo-ocular prolongation; microsculpture of isodiametric mesh, in some specimens obsolescent medially; supra-antennal ridges strongly divergent anteriorly.

Thorax. Pronotum (Fig. 18) with side slightly arcuate to rectilinear or sinuate before posterior angle; posterior angle acute to right and prominent; base lobed; lateral depression complete, becoming wider and shallower posteriorly, in most specimens embracing area of basal fovea; lateral bead becoming less prominent anteriorly; basal bead present laterally; basal fovea shallow, irregular, merging with lateral depression in most specimens; microsculpture of isodiametric mesh, slightly stretched transversely or nearly obsolete medially in some specimens. Mesosternum of some specimens with scattered setae near midcoxa. Metasternum with scattered pubescence near midcoxa.

Legs. Forefemur of most specimens with about 10 setae on posterior margin. Foretibia of most specimens with 5 to 7 spines on distal outer angle (number may vary from side to side on individual specimen). Hindfemur with 2 long setae on posterior margin. Dorsum of all tarsi sparsely pubescent.

Elytron. Intervals flat or slightly convex proximally, more convex distally; subapical sinuation present but not prominent; sutural angle broadly rounded; microsculpture in most specimens appearing as isodiametric slightly granulate mesh, in some specimens as isodiametric punctures at certain light angles.

Abdomen. Tergum VIII of ♀ with obtusely angulate apex (Fig. 55).

Male genitalia. Median lobe (Figs. 91, 92) relatively stout; weakly sclerotized virga on left side of ostium; apex obtusely rounded and with concave area on dorsum. Everted internal sac with 0 to 6 enlarged spine-like scales and with additional varied armature of smaller spines and scales.

*Variation.* — Intrapopulational variation occurs in: body length; coloration of anterior part of clypeus, legs, palpi, and antenna; emargination of labral and clypeal apices; prominence of microsculpture on frons; shape of pronotal base; pubescence of mesosternum; number of setae on posterior margin of forefemur; number of spines along distal outer angle of foretibia; pronotal microsculpture; convexity of elytral intervals; number of enlarged spine-like scales on internal sac; and arrangement and number of smaller spines and scales on internal sac. The variation in number of enlarged spine-like scales is especially noteworthy. In one population (from 3.2 mi. N. Zacatepec, Mexico) I dissected 4 males and found 2 specimens with internal sac lacking enlarged spine-like scales; 1 specimen with a single enlarged spine-like scale; and 1 with 6 enlarged spine-like scales.

*Flight.* — George Ball and his students took 2 males and 2 female at black light in a cut-over palm forest 12.8 mi. E. Manzanillo in August 1967.

*Bionomics.* — Members of *leiroides* have been collected from February to September and at altitudes from sea level to 4,600 feet. Ball's data indicate this species has been taken: in leaf litter near fig tree in tropical deciduous forest 5 mi. E. Tapanatepec, 800 feet; in deep leaf litter on sand to clay loam soil along dry stream bed in mainly tropical deciduous gallery forest 13.8 mi. E. San Blas, 200 feet; in litter of rain forest 2.5 mi. W. Sontecompan, 100 feet; in dry litter and under rocks in mango-zapote orchard at Santa Rosa, 3.2 mi. N. Zanatepec, 3,100 feet; under palm fronds and litter on shaded clay ground in palm forest 12.8 mi. E. Manzanillo, 100 feet; in cut-over palm forest 12.8 mi. E. Manzanillo, sea level; in leaf litter on river banks shaded by large deciduous trees in vicinity of Zanatepec; in leaf



litter in small dry creek bed surrounded by oak forest 37.7 mi. E. Comitan, 2,200 feet; in patch of litter on bare soil near small stream margined with large Mexican cypresses and herbaceous vegetation at Puente Ahuehuyec, 4,200 feet; in litter on dry ground at edge of corn field near small stream in area of former thorn forest at Puente Estudio; and under herbaceous vegetation along road 32.5 mi. E. Comitan, 2,200 feet.

*Distribution and material examined* (167 specimens). This species is known from Mexico, Guatemala, British Honduras, Nicaragua, and Costa Rica (Fig. 151).

#### 10.4 *Notiobia* (*N.*) *limbipennis* H. W. Bates

(Figs. 17, 47, 48, 56, 95, 96, 131, 154)

*Notiobia limbipennis* H. W. Bates, 1878a: 590. [Possible holotype (MNHP), ♀ labeled: "Chontales Nicaragua", "*Notiobia limbipennis* Bates", "Ex-Musaeo H. W. Bates 1892".

TYPE LOCALITY: "Chontales, Nicaragua" as originally cited by Bates. (according to Selander and Vaurie, 1962, Chontales is "Department to the east of Lago de Nicaragua. It formerly extended farther southward to what is now the department of Rio San Juan.").

*Notiobia sinuessa* H. W. Bates, 1882: 56. [Lectotype (BMNH), here designated, ♂ labeled: "Type H. T.", "Type", "Zapote, Guatemala, C. Champion", "B.C.A. Col. I. 1. *Notiobia sinuessa*, Bates ♂". Additional labels added stating: "Lectotype" and "LECTOTYPE *Notiobia sinuessa* Bates By G. R. Noonan". TYPE LOCALITY: Zapote. Guatemala as originally cited. (according to Selander and Vaurie, 1962, = El Zapote in department of Escuintla "Settlement about 12 km. northwest of Escuintla and south of Volcan de Fuego; 2000±feet; 14° 23', 90° 52'.") NEW SYNONYMY].

*Description.* — Body length 9.3 to 12.0 mm.

Color. Dorsum, except labrum and in some specimens anterior part of clypeus which lack tinges and may be lighter in color, with head and pronotum rufobrunneous, rufopiceous to piceous and with greenish, aeneous, or cupreous tinges (tinge may vary over surface of single head or pronotum); elytron of ♂ with greenish, aeneous, or cupreous tinged macula located on inner 7 to 9 intervals proximally and narrowed apically until only inner 2 to 4 intervals so occupied (tinge may vary over surface of single macula). remainder of elytron in ♂ rufopiceous to piceous; elytron in ♀ as in ♂ except macula of many specimens restricted to small apical area. Venter and legs rufobrunneous, rufopiceous to piceous, color may be varied on parts of the same structure. Palpi brunneous, testaceous to rufotestaceous, rufopiceous to piceous. Antenna of most specimens same color as palpi, first segment paler or not.

Head. Labral apex non-emarginate or slightly emarginate medially. Clypeus with apex lobed medially, straight, or moderately broadly emarginate, base of labrum exposed in some specimens; surface smooth to wrinkled. Frons with fovea punctiform, bearing prominent clypeo-ocular prolongation to eye; microsculpture of isodiametric mesh; supra-antennal ridges moderately divergent anteriorly; surface with numerous micropunctures.

Thorax. Pronotum (Fig. 17) with side straight before nearly right posterior angle; lateral depression complete, widened posteriorly and in many specimens embracing area of basal fovea; lateral bead very fine anteriorly; basal bead complete; basal fovea varied, shallow and forming part of posterior portion of lateral depression or deeper and separated from lateral depression by slight convexity; microsculpture as in *melaena*; surface with numerous micropunctures. Prosternum irregularly pubescent. Mesosternum glabrous or with irregular pubescence.

Legs. Forefemur with 4 to 7 setae on posterior margin. Foretibia with 4 to 7 spines on outer distal angle. Dorsum of fore- and midtarsi glabrous to sparsely pubescent. Dorsum of hindtarsus glabrous.

Elytron. Intervals of varied width, with micropunctures, flat to slightly convex proximally, slightly to moderately convex apically; subapical sinuation extremely prominent (in some specimens so prominent as to be angulate exteriorly) especially in ♀ (Figs. 47, 48); sutural angle narrowly rounded; suture with obsolescent to prominent upward projected spine; microsculpture of isodiametric mesh on macula, elsewhere of isodiametric granulate mesh.

Abdomen. Sternum VI of ♀ with apex medially elongated into slightly downward projected spine (Fig. 131). Tergum VIII of ♀ with angulate apex (Fig. 56).

Male genitalia. Median lobe (Figs. 95, 96) with moderately sclerotized virga present to left of ostium; apex short. Everted internal sac with varied fields of small scales and with or without varied field of enlarged spine-like scales; internal sac in repose with the field of enlarged spine-like scales visible or not in median area of ventral side of shaft.

Female genitalia. Stylus dorso-ventrally flattened, without concave area on dorso-lateral side.

*Variation.* — Intrapopulational variation occurs in: body size; body color; extent of macula on elytron; presence or absence of emargination of labral apex; shape of clypeal apex; surface texture of clypeus; pronotal lateral depression and basal fovea; mesosternal pubescence; number of setae on posterior margin of forefemur and number of spines on outer distal angle of foretibia (number of setae and spines may vary from side to side in same specimen); dorsal pubescence of fore- and midtarsi; convexity and relative width of elytral intervals; degree of prominence of elytral subapical sinuation and sutural spine; and armature of internal sac.

*Discussion.* — The possible holotype of *limbipennis* at the MNHP is a female. However, at the end of his original description Bates stated "Long  $5\frac{1}{2}$  lin. ♂. Hab. Chontales, Nicaragua (Belt)." The description refers to the elytron as having a prominent subapical sinuation which might indicate Bates was describing a female rather than a male since the subapical sinuation is more prominent in the female. The BMNH does not contain any specimens identifiable as types of *limbipennis*, and the Bates boxes in the Oberthür collection at MNHP contain a total of 2 specimens of *limbipennis*: the above-mentioned female and a female labeled "Bakia", "Ex-Musaeo H. W. Bates 1892". The female from Chontales, Nicaragua fits the original description, except for the portion stating the type to be a male, and probably is the true holotype.

The form *sinuessa* was according to Bates (1882) "... distinguished by its smaller size, darker coppery or brassy-brown colour (which is not changed to tawny on the alutaceous patches of the elytra), and by the upper end of the elytral sinuation not forming a sharp angle." These characters all vary within populations, and there is no valid reason to retain *sinuessa* as a separate species.

*Flight.* — George Ball and D. R. Whitehead took 2 males and 2 females at black light in a tropical montane forest 11.6 mi. N. Ocozocautla in June 1966.

*Bionomics.* — Members of this species have been taken during June to August and at altitudes ranging from 140 to 2,700 feet. Ball's data indicate this species has been taken: under rock in partly shaded area in mixed deciduous woods 7.5 mi. E. Chiapa de Corzo, 2,700 feet; under herbaceous vegetation along road 32.5 mi. E. Comitán, 2,200 feet; and in forest with palms predominant, few very large bromeliads and rich understory of vegetation 5.7 mi. E. San Blas, 140 feet.

*Distribution and material examined* (82 specimens). This species has been taken from scattered localities in Mexico, Guatemala, Nicaragua, Costa Rica, Panama, (Fig. 154) and also from French Guiana, Peru, and Tobago.

10.5 *Notiobia (N.) melaena* H. W. Bates  
(Figs. 20, 59, 93, 94, 149)

*Notiobia melaena* H. W. Bates, 1882: 54. [Lectotype (BMNH), here designated, ♂ labeled: "Type H. T.", "Cordova", "Mexico Salle Coll.", "B.C.A. Col. I. 1. *Notiobia melaena* Bates", "*Notiobia melaena* Bates ♂". Additional labels added stating: "Lectotype" and "LECTOTYPE *Notiobia melaena* Bates By G. R. Noonan". TYPE LOCALITY: Cordova, Veracruz, Mexico as originally cited].

*Notiobia aequata* H. W. Bates, 1882: 54. [Holotype (BMNH), ♀ labeled: "Type H. T.", "Cordova", "Mexico, Salle Coll.", "Type", "B.C.A. I. 1. *Notiobia aequata*, Bates.", "*Notiobia aequata* Bates". TYPE LOCALITY: Cordova, Veracruz, Mexico as originally cited. NEW SYNONYMY].

*Description.* — Body length 10.4 to 10.9 mm.

Color. Dorsum with labrum rufous, remainder black, some specimens with purple or violaceous tinge on dorsum. Venter rufopiceous to black. Foreleg rufous to black. Midleg with tarsus and trochanter of most specimens rufous and remainder black. Hindleg rufous to black except tarsus not darker than rufopiceous. Palpi rufotestaceous. Antenna with first 4 segments independently varied from rufous to black except for rufous bases and apices.

Head. Labral apex slightly to moderately emarginate medially. Clypeal apex slightly to prominently broadly emarginate medially and in some specimens base of labrum exposed. Frons with fovea punctiform, bearing prominent clypeo-ocular prolongation to eye; microsculpture of isodiametric mesh, in some specimens obsolescent medially; supra-antennal ridges only slightly divergent anteriorly.

Thorax. Pronotum (Fig. 20) with side straight to prominently sinuate before posterior angle; posterior angle right to acute and slightly projected; lateral depression complete, shallower and wider posteriorly, in some specimens embracing area of basal fovea; lateral bead extremely prominent, especially posteriorly; basal bead complete; basal fovea various; microsculpture of isodiametric mesh, slightly stretched medially.

Legs. Forefemur with 4 to 7 setae on posterior margin. Foretibia with 2 spines in ♂ and 3 to 5 spines in ♀ on outer distal angle (number of setae on femur and number of spines on tibia in ♀ may vary from side to side on individual specimen). Dorsum of tarsi glabrous except for occasional spine-like seta.

Elytron. Intervlas flat to slightly convex; subapical sinuation slight; sutural angle broadly rounded; microsculpture of isodiametric or transversely stretched mesh.

Abdomen. Tergum VIII of ♀ with obtusely rounded apex (Fig. 59).

Male genitalia. Median lobe (Figs. 93, 94) with apex bent slightly ventrad. Internal sac in repose with prominent elongate spine visible beneath membranous dorsal area of median lobe; everted sac with the prominent elongate spine proximal to median lobe and with small scattered spine-like scales.

*Discussion.* — The form *aequata* was proposed by Bates as having elytral intervals flatter and posterior angle of pronotum more prominent. As noted in the description these characters vary within the species *melaena*, and the type of *aequata* falls within the normal limits of variation of these characters in *melaena*.

*Flight.* — George Ball and D. R. Whitehead took 1 female *melaena* at black light 11.6 mi. N. Ocozocuahtla in a tropical montane forest in June, and D. R. Whitehead took 1 male by black light at Fortin de las Flores in June.

*Bionomics.* — Specimens of *melaena* have been taken in June, August to October and at altitudes from 2,900 to 5,000 feet. Ball's data indicate they have been taken: in leaf litter near banks of river in partly cut-over evergreen tropical forest at Fortin de las Flores, 2,900

feet; and under rotten log near big elephant ear plant in heavily shaded section of oak-sweet gum forest at Sierra de Guatemala, 8.1 mi. W. Encino.

*Distribution and material examined* (22 specimens). This species occurs in southern Mexico and Guatemala (Fig. 149).

### 10.6 *Notiobia* (*N.*) *obscura* H. W. Bates

(Figs. 24, 50, 51, 99, 100, 152)

*Notiobia obscura* H. W. Bates, 1882: 53. [Lectotype (BMNH), here designated, ♀ labeled: "Playa Vicente, Mexico. Salle. Coll", "B.C.A. Col. I. 1. *Notiobia obscura*, Bates.". Additional labels added stating: "Lectotype" and "LECTOTYPE *Notiobia obscura* Bates By G. R. Noonan". TYPE LOCALITY: Playa Vicente, Veracruz, Mexico as originally cited].

Var. *virens* H. W. Bates, 1882: 53.

*Description.* — Body length 7.2 to 9.5 mm.

Color. Dorsum with labrum and in some specimens anterior part of clypeus rufous to piceous; remainder of head and pronotum rufopiceous to piceous, in some specimens with slight cupreous or greenish tinge; elytron rufopiceous to piceous, in most specimens with distinct greenish or aeneous tinge. Venter rufopiceous to piceous. Legs of most specimens testaceous to rufotestaceous, in a few specimens rufopiceous, in some specimens with coxa, trochanter, base of femur, and tarsus lighter than other parts. Palpi rufotestaceous to rufopiceous. Antenna rufotestaceous.

Head. Labral apex slightly emarginate medially (Fig. 51). Clypeus with apex slightly to moderately broadly emarginate, in some specimens base of labrum exposed; surface slightly wrinkled. Frons with fovea punctiform, bearing faint short clypeo-ocular prolongation not reaching eye; microsculpture of isodiametric mesh, obsolescent medially; supra-antennal ridges only slightly divergent anteriorly.

Thorax. Pronotum (Fig. 24) with side slightly to moderately sinuate before posterior angle; posterior angle prominent, slightly to moderately projected, acute; base lobed; lateral depression shallow, incomplete, becoming obsolete posteriorly; lateral bead becoming less prominent anteriorly; basal bead complete; basal fovea varied, obsolete in some specimens; microsculpture of isodiametric mesh, obsolescent medially in some specimens.

Legs. Forefemur with 3 to 7 setae on posterior margin. Foretibia with 2 spines in ♂ and 4 in ♀ on outer distal margin. Dorsum of laterally dilated segments in ♂ fore- and midtarsi glabrous to sparsely pubescent, dorsum of segment V glabrous. Dorsum of all tarsi in ♀ and hindtarsus in ♂ glabrous.

Elytron. Intervals flat; subapical situation slight (Fig. 50); sutural angle rounded; microsculpture of isodiametric mesh.

Abdomen. Tergum VIII of ♀ with obtusely rounded apex as in *melaena*.

Male genitalia. Median lobe as in Figs. 99, 100. Internal sac in repose with prominent elongate spine visible in distal portion of dorsal membranous area of median lobe; everted sac with the prominent elongate spine located proximal to median lobe and with fields of small spine-like scales.

*Discussion.* — The name *virens* was mentioned by Bates as being based on specimens from Cordova, Mexico, labeled with this name in the Salle collection. These specimens were distinguished from other *obscura* by having the pronotal posterior angle slightly more prominent. However, variation occurs in the prominence of this angle, and there is no reason to validate the name *virens*.

*Bionomics.* — Members of *obscura* have been taken in February, May, and July and at altitudes from 1,000 to 6,000 feet. Ball's data indicate specimens have been taken: in deep

litter on black rich loam soil in cool, densely shaded ravine with tropical vegetation 33.7 mi. N. Huixtla, 6,000 feet; under banana log in banana plantation located in pine-oak zone 18.4 mi. S. Suchixtepec, 4,500 feet; and in damp, deep litter in vicinity of dried pond inside cloud forest with very dense canopy 16.9 mi. S. Valle Nacional, 3,600 feet.

*Distribution and material examined* (15 specimens). This species is found in southern Mexico (Fig. 152).

#### 10.7 *Notiobia* (*N.*) *pallipes* H. W. Bates

(Figs. 21, 52, 101, 102, 156)

*Notiobia pallipes* H. W. Bates, 1882: 53. [Lectotype (BMNH), here designated, ♂ labeled: "Type H. T.", "Type", "Oaxaca, Mexico. Hoege.", "B.C.A. Col. I. 1. *Notiobia pallipes*, Bates", "*Notiobia pallipes* Bates ♂". Additional labels added stating: "Lectotype" and "LECTOTYPE *Notiobia pallipes pallipes* Bates By G. R. Noonan". TYPE LOCALITY: Type material originally stated to be from Cordova, Jalapa, and Oaxaca in Mexico. Type locality here restricted to Oaxaca, Oaxaca, Mexico].

Var. *subaurata* H. W. Bates, 1882: 53. [Holotype (BMNH), ♂ labeled: "Holotype", "Capetillo, Guatemala, G. C. Champion.", "B.C.A. Col. I. 1. *Notiobia pallipes*, v. *subaurata*, Bates", "*Notiobia pallipes* v. *subaurata*". Additional label added stating: "Holotype *Notiobia pallipes subaurata* Bates det. G. Noonan 1970". TYPE LOCALITY: Capetillo, Guatemala as originally cited. NEW SYNONYMY].

*Description.* — Body length 8.2 to 9.5 mm.

Color. Dorsum with labrum and in some specimens anterior part of clypeus rufous or rufopiceous, remainder rufopiceous, with prominent greenish tinge. Venter rufopiceous. Legs with coxae testaceous, brunneous, or rufopiceous, remainder testaceous. Palpi testaceous. Antenna testaceous to rufotestaceous.

Head. Labral apex prominently emarginate medially. Clypeal apex broadly emarginate medially and in some specimens base of labrum exposed. Frons with fovea punctiform, bearing prominent clypeo-ocular prolongation to eye; microsculpture of isodiametric mesh; supra-antennal ridges strongly divergent anteriorly.

Thorax. Pronotum (Fig. 21) with side rectilinear or sinuate before posterior angle; posterior angle right and prominent or obtuse and not prominent, slightly projected in some specimens; lateral depression complete, shallower and slightly wider posteriorly; basal fovea shallow, not distinctly defined; microsculpture of isodiametric mesh, in some specimens slightly transversely stretched medially. Metasternum with few short fine setae near junction with mesosternum.

Legs. Forefemur with 3 to 5 setae on posterior margin. Foretibia with 2 in ♂ and 3 to 4 spines in ♀ on outer distal angle (number of spines may vary from side to side on individual ♀). Dorsum of tarsi glabrous except for occasional spine-like seta.

Elytron. Intervals flat except slightly convex near apex; subapical sinuation slight; sutural angle broadly rounded; microsculpture of isodiametric mesh.

Abdomen. Tergum VIII of ♀ with obtusely rounded apex (Fig. 52).

Male genitalia. Median lobe (Figs. 101, 102) with shaft markedly constricted (in dorsal view) just before apex. Internal sac in repose with prominent elongate spine visible beneath distal portion of median lobe membranous dorsal area; everted sac with the prominent elongate spine proximally located and with fields of scales and small spines.

*Variation.* — Intrapopulational variation occurs in: body length; coloration of anterior part of clypeus, coxae, and antenna; emargination of clypeal apex; shape of pronotal side; pubescence of metasternum; number of setae on posterior margin of forefemur; and number

of spines on outer angle of foretibia in females.

*Discussion.* — The form *subaurata* was described on the basis of a single male from Capetillo, Guatemala and characterized by having the pronotal side sinuate just before the acute and slightly projected posterior angle. The few specimens I have seen from Guatemala do indeed have this type of pronotum. Most Mexican specimens have the posterior angle more obtuse and non-projected while the pronotal side is usually straight or very slightly sinuate before the posterior angle. However, the shape of this angle and the sinuation of the side vary within populations in Mexico. Therefore, I do not recognize *subaurata* as a valid subspecies.

*Flight.* — George Ball and D. R. Whitehead have taken this species at black light in June: at Fortin de las Flores; and in a tropical montane forest 11.6 mi. N. Ocozocuatla.

*Bionomics.* — Members of *pallipes* have been taken in January, March to June, and August and at altitudes from 2,624 to 4,700 feet. Ball's data indicate specimens have been taken: from bromeliads on south-facing slope of pasture in badly cut-over area once probably predominantly of *Liquidamber* forest 10.4 mi. S. W. Huatusco, 4,700 feet; from bromeliad in partly cut-over tropical evergreen forest at Fortin de las Flores, 2,900 feet; and by washing deep, rich leaf litter located within a few feet of river at Fortin de las Flores.

*Distribution and material examined* (63 specimens). This species occurs in southern Mexico (Fig. 156). I have also seen 2 specimens from Guatemala.

#### 10.8 *Notiobia* (N.) *parilis* H. W. Bates

(Fig. 153)

*Notiobia parilis* H. W. Bates, 1878 a: 590. [Lectotype (MNHP), here designated, ♂ labeled: "Chontales Nicaragua". Additional label added stating: "LECTOTYPE *Notiobia parilis* Bates By G. R. Noonan". TYPE LOCALITY: Chontales, Nicaragua as originally cited (according to Selander and Vaurie 1962, = department to east of Lago de Nicaragua, formerly extended farther southward to what is now department of Rio San Juan)].

*Description.* — Body length 11.3 to 13.1 mm.

Color. Mexican morph. Dorsum with labrum and anterior part of clypeus in some specimens rufous to rufopiceous, in other specimens piceous and with distinct purple tinge as in rest of dorsum. Venter and legs rufopiceous to piceous. Palpi rufopiceous to piceous or infuscated. Antenna rufopiceous to piceous; one or more of first 3 segments may be lighter than more distal ones.

Color. Panamanian morph. Dorsum with labrum and in some specimens anterior part of clypeus rufous to rufopiceous or else clypeus same color as rest of dorsum of head; head and pronotum green, aeneous, or cupreous. Elytron purple or bluish purple. Venter and legs piceous in most specimens, rufopiceous in a few specimens, with slight irregular greenish tinge. Palpi same as in Mexican morph. Antenna piceous in most specimens, rufopiceous in a few specimens; one or more of first 3 segments may be lighter than more distal ones.

Head. As in *leiroides*, except clypeo-ocular prolongation present in some specimens.

Thorax. As in *leiroides*.

Legs. As in *leiroides*.

Elytron. As in *leiroides* except that intervals of elytron are moderately convex proximally.

Abdomen. As in *leiroides*.

Male genitalia. Median lobe as in *leiroides*. Internal sac with armature of small spines and scales as in *leiroides*; no enlarged spine-like scales present.

*Variation.* — I did not examine enough specimens to evaluate all of the variation shown by this species. However, it is apparent that intrapopulational variation exists in the: degree of

emargination of clypeal apex and shape of basal part of pronotum.

The coloration of the body shows interesting geographical variation. Specimens from Mexico have the dorsum with the proximal part of the head and all of the pronotum and elytron bearing a conspicuous purplish tinge. Specimens with this color state are here referred to as the "Mexican morph". The Mexican morph extends into Central America, and the following specimens from there belong to this morph: 1 male, 3 females from Chontales, Nicaragua; 1 female from San Jose, Costa Rica; and 2 males, 1 female from Costa Rica. In Central America, variation in body color occurs and there is found a second form, here termed the "Panamanian morph", in which the head and pronotum of most specimens differ in color from the elytron. The venter and legs also have a faint irregular greenish tinge, and the appendages are usually darker in color than in the Mexican morph. Five color combinations are outlined in Table 1 (p. 428). These color combinations show a definite tendency to intergrade, and it is often difficult to decide in which category a specimen belongs; and more than one color combination may occur at a single locality. Thus, this color variation is probably intrapopulational in nature; additional collecting is needed to completely determine the nature of this variation.

*Discussion.* — The BMNH contains 1 *parilis* labeled: "Type H. T.", "Playa Vicente", "Mexico Salle Coll", "B.C.A. Col. I. 1. Notiobia parilis. Bates.", "Notiobia parilis ♂ Bates". This specimen cannot be a syntype since it is not from the type locality originally cited by Bates.

*Flight.* — George Ball and his students have collected *parilis* at black light in a tropical montane forest 11.6 mi. N. Ocozocuatla in June 1966 and at Fortin de las Flores in May 1966.

*Bionomics.* — Members of this species have been collected in February, April to June, August to September, and at altitudes from 0-100 to 3,200 feet. Ball's data indicate *parilis* has been taken: in leaf litter of lowland rain forests in the vicinity of Sontecompan and at the Palenque ruins; in leaf litter near banks of river in partly cut-over tropical evergreen forest at Fortin de las Flores, 2,900 feet; and in densely shaded leaf litter in mountain rain forest at San Quintin, Sierra de la Colmena, approximately 300-700 feet.

*Distribution and material examined* (72 specimens). This species is known from southern Mexico, Central America, (Fig. 153) and São Paulo (whether city or province not certain) Brazil. I have seen 1 male labeled "Amazonas" which probably refers to 1 of 3 areas named "Amazonas" in Colombia, northern Brazil, or Peru.

#### 10.9 *Notiobia (N.) umbrata* H. W. Bates

(Figs. 25, 49, 53, 105, 106, 155)

*Notiobia umbrata* H. W. Bates, 1882: 55. [Lectotype (BMNH), here designated, ♂ labeled: "Zapote, Guatemala C. Champion", "B.C.A. Col. I. 1. Notiobia umbrata Bates.", "Notiobia umbrata Bates". Additional labels added stating: "Lectotype" and "LECTOTYPE Notiobia umbrata Bates By G. R. Noonan". TYPE LOCALITY: Zapote, Guatemala as originally cited (according to Selander and Vaurie, 1962 = El Zapote, Department of Escuintla, "settlement about 12 km. northwest of Escuintla and south of Volcan de Fuego: 2000± feet; 14° 23', 90° 52'.")].

*Description.* — Body length 8.4 to 9.7 mm.

Color. Dorsum with labrum and anterior part of clypeus rufous to rufopiceous; remainder of head and pronotum rufopiceous to piceous and with distinct prominent greenish tinge or slightly less prominent cupreous tinge; elytron of ♂ with greenish tinged macula in most specimens on inner 9 intervals proximally and narrowed apically until only inner 2 to 4 inter-

vals so covered; remainder of elytron of ♂ rufopiceous to piceous; elytron of ♀ completely rufopiceous to piceous or with various proximal and distal greenish tinged maculae on inner intervals. Venter rufopiceous to piceous; abdominal sterna (especially apical ones) of most specimens with sides testaceous or brunneous, apex of sternum VI of most specimens testaceous or brunneous. Legs testaceous except hindcoxa of most specimens rufopiceous. Palpi testaceous to brunneous. Antenna same color as palpi.

Head. Labral apex not emarginate. Clypeus with apex broadly emarginate medially or wavy, base of labrum exposed in most specimens; surface wrinkled near apex. Frons with fovea punctiform, bearing clypeo-ocular prolongation to eye; microsculpture of isodiametric mesh; supra-antennal ridges strongly divergent anteriorly.

Thorax. Pronotum (Fig. 25) with side straight or very slightly sinuate before posterior angle; posterior angle acute to slightly obtuse; base lobed; lateral depression complete, widened posteriorly; lateral bead less prominent anteriorly; basal bead complete; basal fovea shallow, not distinctly defined; microsculpture of isodiametric mesh. Prosternum sparsely pubescent with short fine setae.

Legs. Forefemur with 3 to 7 setae on posterior margin. Foretibia with 3 to 4 spines on outer distal angle (number of spines may vary from side to side on individual specimen). Dorsum of segments I to IV of fore- and midtarsi of ♂ pubescent; dorsum of segment V of ♂ glabrous. Dorsum of all tarsi of ♀ and of hindtarsus of ♂ glabrous.

Elytron. Scutellar stria extremely long (length scutellar stria/length elytron greater than 0.3); intervals flat except slightly convex near apex; subapical sinuation slight to moderate; sutural angle broadly rounded; microsculpture of isodiametric mesh, granulate isodiametric mesh, or isodiametric punctures.

Abdomen. Tergum VIII of ♀ with obtusely rounded apex (Fig. 53).

Male genitalia. Median lobe (Figs. 105, 106) with apex short. Internal sac not examined in everted position due to lack of mature ♂♂; no armature visible through walls of median lobe.

*Flight*. — George Ball and D. R. Whitehead have taken *umbrata* at black light: in a tropical montane forest 11.6 mi. N. Ocozocuatla in June; and in a montane rain forest in hills 5 to 6 miles away from Lake Catemaco in July.

*Bionomics*. — Members of *umbrata* have been collected from June to July and at altitudes from 100 to 4,700 feet. Ball's data indicate specimens have been taken: in deep leaf litter on sandy to clay loam soil along dry stream bed in mainly tropical deciduous gallery forest 0.9 mi. N. Frontera Comalapa. 2,100 feet; inside densely shaded lowland rain forest 2.5 mi. W. Sontecompan. 100 feet; and in densely shaded leaf litter in lowland rain forest at Palenque ruins. 400 feet.

*Distribution and material examined* (17 specimens). This species occurs in southern Mexico and Guatemala (Fig. 155).

#### 10.10 *Notiobia* (*N.*) *umbrifera* H. W. Bates

(Figs. 23, 54, 97, 98, 148)

*Notiobia umbrifera* H. W. Bates. 1884: 271. [Lectotype (BMNH), here designated, ♂ originally glued on single card with ♀ paralectotype. Lectotype now pinned and bearing following labels formerly on pin holding both specimens: "Type H. T.", "Bugaba Panama Champion.", "B.C.A. Col. I. 1. *Notiobia umbrifera* Bates.", "*Notiobia umbrifera* Bates". Additional labels added stating: "Lectotype" and "LECTOTYPE *Notiobia umbrifera* Bates By G. R. Noonan". Paralectotype ♀ now bears handwritten label duplicating information on original labels and handwritten label stating that ♀ was formerly on same card as lectotype. TYPE LOCALITY: Bugaba, Panama and Upper Amazons, South America



originally cited, here restricted to Bugaba, Panama (Bugaba, according to Selander and Vaurie, 1962, = settlement about 22 km. northwest of David, 1,000 feet, 8° 28', 82° 38').

*Description.* — Body length 7.3 to 8.4 mm.

Color. Dorsum with labrum and anterior part of clypeus testaceous, rufous to rufopiceous; remainder of head and pronotum rufopiceous to piceous and with greenish or aeneous tinge; elytron of both sexes with greenish or aeneous tinged macula occupying in most specimens inner 8 to 9 intervals proximally, narrowed apically until only inner 2 to 4 intervals so covered, remainder of elytron rufous to rufopiceous. Venter with thorax rufous to piceous; abdominal sterna testaceous to rufous to brunneous medially, rufopiceous to piceous laterally in most specimens. Legs as in *umbrata*. Palpi testaceous to rufotestaceous, rufous to rufopiceous, or brunneous. Antenna same color as palpi.

Head. As in *umbrata* except dorsum wrinkled near clypeus.

Thorax. Pronotum (Fig. 23) with side straight or very slightly sinuate before prominent posterior angle; base lobed; lateral depression not prominent, wider and obsolete posteriorly; lateral bead narrowed anteriorly; basal bead present laterally, obsolete medially; basal fovea obsolete; microsculpture of isodiametric mesh, in some specimens slightly transversely stretched medially.

Legs. Forefemur with 3 to 7 setae on posterior margin. Foretibia with 3 to 5 spines on outer distal angle (number of setae on femur and number of spines on tibial outer angle may vary from side to side on individual specimen). Dorsum of segments I to IV of ♂ fore- and midtarsi pubescent; dorsum of segment V glabrous. Dorsum of all tarsi in ♀ and of hindtarsus in ♂ glabrous.

Elytron. Scutellar stria moderately long; intervals flat except near apex; subapical sinuation moderate; sutural angle broadly rounded; microsculpture of isodiametric mesh on macula and of granulate isodiametric mesh or isodiametric punctures elsewhere.

Abdomen. Tergum VIII of ♀ with angulate apex. (Fig. 54).

Male genitalia. Median lobe (Figs. 97, 98) with apex very elongate, in many specimens curved leftward. Internal sac in repose bearing prominent large spine visible beneath dorsal membranous area of median lobe; dissected internal sac bearing several elongate small spines in addition to the prominent large spine.

Female genitalia. Stylus compressed medio-laterally and somewhat lobe-like.

*Variation.* — Intrapopulational variation occurs in: body color; emargination of clypeal apex; shape of pronotal base; number of setae on posterior margin of forefemur; number of spines along distal outer margin of foretibia; pronotal microsculpture; elytral microsculpture; and curvature of median lobe apex.

*Flight.* — Members of this species have been taken at lights on Barro Colorado Island, Canal Zone, Panama.

*Bionomics.* — All specimens bearing dated labels were collected between April and November.

*Distribution and material examined* (56 specimens). Bates (1884) cited specimens from Panama and Upper Amazons, South America. I have seen material only from Panama (Fig. 148), but additional collecting may reveal that it does extend into South America.

## 11 subgenus *Diatypus* Murray NEW STATUS

(Figs. 210, 211)

*Diatypus* Murray, 1858: 343. [TYPE SPECIES: *Diatypus dohrni* Murray, 1858 (according to Basilewsky, 1950)].

*Dichiropsis* Jeannel, 1946: 157. [TYPE SPECIES: *Anisodactylus picinus* Chaudoir, 1878, by

original designation].

*Paradiatypus* Basilewsky, 1950: 19. [TYPE SPECIES: *Diatypus smithi* Murray 1858, by original designation. NEW SYNONYMY].

*Description.* — Body of most specimens piceous to black, but in some specimens with metallic tinges on dorsum.

Head. Labral apex slightly to moderately emarginate medially. Frontal fovea punctiform, with or without clypeo-ocular prolongation. Eye large and protruding. Gena (except in few species of "*Paradiatypus*" species group) narrow with narrowest part between margin of eye and mouth much narrower than maximum width of first antennal segment. Ligula narrow and not expanded laterally at apex in "*Diatypus*" species group; broader and strongly expanded laterally at apex in "*Paradiatypus*" species group. Paraglossa wide and longer than ligula in "*Diatypus*" species group; narrow and shorter than ligula in "*Paradiatypus*" species group.

Legs. Foretibia with distal portion moderately expanded laterally; apical spur lanceolate. Hindtarsus with segment I shorter or equal to II + III. Dorsum of all tarsi glabrous. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Intervals convex in most specimens; interval III with 3 to many dorsal setigerous punctures; interval VII with minute ocellate puncture at extreme apex and large prominent ocellate puncture slightly more proximally located.

Hind wing. Various in size.

Abdomen. Sternum VI of ♂ with 1 or 2 pairs of ambulatory setae.

Male genitalia. Median lobe with apex narrow, bearing "button"-like disc (Figs. 210, 211).

*Discussion.* — The reasons for regarding *Diatypus* as a subgenus of *Notiobia* rather than as a separate genus are reviewed in the discussion section on the genus *Notiobia*. Basilewsky (1950) provided a thorough review of why *Dichiropsis* must be regarded as congeneric with *Diatypus*, and I agree fully with him in this decision. Basilewsky (1950) proposed *Paradiatypus* as a subgenus of the then separate genus *Diatypus*. I here treat the former subgenus *Paradiatypus* as a species group of the subgenus *Diatypus*.

The subgenus is composed of 2 species groups defined by ligula and paraglossa characters listed in the genus description. The species of both groups are found in tropical portions of Africa. The 3 "*Diatypus*" group species are: *diffusus* (Klug), 1833; *dohrni* Murray, 1858 ♀\*; and *picinus* (Chaudoir), 1878. The 7 "*Paradiatypus*" group species are: *bamboutensis* Basilewsky, 1948\*; *elongensis* Basilewsky, 1948\*; *feanus* Basilewsky, 1949\*; *kivuensis* Burgeon, 1936 ♀\*; *leonensis* Basilewsky, 1949 ♀\*; *ruwenzoricus* Burgeon, 1936 ♀\*; and *smithi* Murray, 1858 ♀\*.

## 12 genus *Anisostichus* van Emden NEW STATUS

(Fig. 175)

*Anisostichus* van Emden, 1953: 520. [(as subgenus of *Anisotarsus*) TYPE SPECIES: *Harpalus laevis* Curtis, 1839 by original designation].

*Description.* — Body length 6.3 to 8.6 mm.

Color. Various.

Head. Labral apex slightly to moderately emarginate medially. Clypeal apex slightly to moderately emarginate medially, in some specimens base of labrum exposed. Frons with obsolete or very small punctiform fovea lacking clypeo-ocular prolongation; microsculpture of isodiametric mesh (obsolete medially in *amoenus*); supra-antennal ridges slightly to moderately divergent anteriorly; narrowest width of gena wider than maximum width of first

antennal segment. Mentum with prominent tooth. Mentum and submentum fused, only groove indicating former separating suture (groove somewhat deeper in *octopunctatus* and *posticus*). Ligula (Fig. 175) narrow, not expanded at apex. Paraglossa (Fig. 175) subequal in length to ligula.

Thorax. Pronotum moderately convex; slightly cordate to rectangular in shape; base straight to slightly lobed; lateral depression obsolete; lateral bead complete, not prominent; basal bead complete in most specimens, obsolete medially; apical bead present laterally; basal fovea obsolescent; microsculpture of isodiametric mesh, slightly transversely stretched medially (except obsolete medially in *amoenus*). Prosternum irregularly, sparsely pubescent. Metasternum with or without scattered pubescence. Mesosternum of most specimens sparsely pubescent. Remainder of venter glabrous.

Legs. Foretibia with apical spur lanceolate. Hindfemur with 2 long setae on posterior margin, except 3 to 5 in *amoenus*. Hindtarsus with segment I shorter than II + III. Dorsum of all tarsi glabrous to pubescent. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with segments II to IV and also in some specimens apex of segment I laterally expanded and spongy pubescent beneath.

Elytron. Humerus with or without small tooth; scutellar stria long and capturing distal portion of stria I in many specimens; intervals flat to slightly convex; interval III with 3 to 6 setigerous punctures extended from apex to or nearly to base; interval VII with minute setigerous sub-ocellate puncture near apex and slightly more proximal ocellate puncture; sub-apical sinuation obsolescent; stria in *amoenus* weak or obsolescent except for first, normal in other species; microsculpture in *amoenus* of transverse mesh, in *laevis* and *octopunctatus* of isodiametric mesh, in *posticus* of slightly transverse isodiametric mesh.

Hind wing. Full and apparently functional in all species.

Abdomen. Sternum VI with 2 pairs of ambulatory setae in ♂, 1 pair in occasional specimens of *laevis*. Apex of ♀ tergum VIII obtusely angulate to broadly rounded.

Male genitalia. Median lobe with membranous area of dorsum reaching basal bulb in *octopunctatus* and *posticus*, short and not reaching basal bulb in *amoenus* and *laevis*. Internal sac in repose with elongate spine visible in region of ostium of median lobe.

Female genitalia. Valvifer similar to that of *Notiobia*; weakly sclerotized, slightly convex; lateral distal margin partly membranous and without discrete boundary.

*Discussion.* — This group was proposed as a subgenus of *Anisotarsus* by van Emden (1953). However it merits separate status from *Notiobia* (*s. str.*) and *Diatypus* because of the fused mentum and submentum. And the series of setigerous punctures on the third elytral interval distinguish its species from those of *Anisotarsus* and *Notiobia* (*s. str.*).

The 4 species of *Anisostichus* occur in temperate areas of South America and are: *amoenus* (Solier), 1849; *laevis* (Curtis), 1839; *octopunctatus* (Dejean), 1829, and *posticus* (Dejean), 1829. Van Emden (1953) provided a key to these species.

### 13 genus *Scybalicus* Schaum

(Figs. 183, 208, 209, 216)

*Scybalicus* Schaum, 1862: 118. [TYPE SPECIES: *Harpalus oblongiusculus* Dejean, 1829 by monotypy].

*Apatelus* Schaum, 1860: 560. [preoccupied by *Apatelus* Mulsant and Rev. 1859. TYPE SPECIES: *Harpalus oblongiusculus* Dejean, 1829, by monotypy].

*Description.* — Body length 12 to 14 mm. Body somewhat elongate in form and with dense pubescence.

Color. Body brown to black.

Head. Labral apex prominently emarginate medially. Frontal fovea varied (within species) from obsolete to moderate sized and deep, with or without slight clypeo-ocular prolongation. Antenna moderately long, exceeding pronotal base. Mentum with obtuse tooth. Mentum and submentum separated by complete transverse suture. Submentum with various setae of different length and thickness. Ligula slender; dorsal surface with several very fine short setae in *hirtus*, glabrous in *oblongiusculus*. Paraglossa slightly longer than ligula.

Thorax. Pronotum (Fig. 183) semicordate; lateral depression obsolescent; lateral bead present anteriorly but in many specimens obsolescent towards posterior angle; apical bead present only laterally; basal bead absent or suggestion of bead present laterally near posterior angle.

Legs. Foretibial apical spur dilated near base or angulate at sides. Foretarsus of ♂ with at least segment II to IV slightly laterally expanded and spongy pubescent beneath. Midtarsus of ♂ various. Hindtarsus with segment I as long or longer than II + III.

Elytron. Scutellar stria moderately long and in some specimens distally reaching stria I; all intervals densely pubescent.

Male genitalia. Median lobe of *oblongiusculus* (Figs. 208, 209) with apex deflected to right and bearing moderate apical disc; membranous area of dorsum somewhat indistinct; ventral surface unmodified.

Female genitalia. Valvifer (Fig. 216) moderately sclerotized, flattened, with several distal setae.

*Discussion.* — The genus *Scybalicus* contains 3 species: *biroi* Jedlicka, 1952\*, described from Dijarbekir, Asia Minor; *kabylianus* Reiche, 1861\*, found in mountains of northeastern Algeria and northwestern Tunisia; and *oblongiusculus* (Dejean), 1829, found in England, southern Europe, and northern Africa.

To prevent possible further confusion the form of the median lobe of *oblongiusculus* (Figs. 208, 209) will be briefly discussed here. Jeannel (1942a) described the ventral border as being equipped with a "sorte de carène lamelleuse longitudinale". As pointed out by Antoine (1959), and confirmed by myself the ventral border does not possess such a structure and is unmodified.

#### 14-15 genus *Progonochaetus* G. Müller

*Progonochaetus* G. Müller, 1938: 245. [TYPE SPECIES: *Anisodactylus xanthopus* Dejean, 1829, by original designation].

*Description.* — Body length 9 to 11 mm.

Color. Body of most specimens black to piceous; elytron of some specimens with slight bronze tinge.

Head. Labral apex straight to moderately emarginate medially. Clypeal apex straight to slightly emarginate medially. Mentum lacking tooth. Mentum and submentum separated medially by transverse suture; such suture obliterated laterally in many specimens; state of suture laterally varied within some species. Ligula narrow; with or without distal dorsal setae. Paraglossa various in length, with setae on dorsal base and in many specimens with setae along mesal and dorso-mesal sides (setae may be difficult to discern in some species).

Pronotum with 2 lateral seta, 1 near middle and 1 towards posterior angle; lateral bead complete; apical and basal beads present at least laterally.

Legs. Foretibia with distal portion moderately expanded laterally; apical spur lanceolate. Hindfemur of most specimens with 2 long setae on posterior margin. Hindtarsus with segment I shorter to longer than II + III. Dorsum of all tarsi pubescent in most specimens.

Elytron. Scutellar stria unmodified or in some specimens long and joined distally with interval I; intervals flat to slightly convex; interval III and in some specimens interval VII with several dorsal setigerous punctures; interval VII with minute ocellate puncture at extreme apex and large prominent ocellate puncture slightly more proximally located.

Abdomen. Sternum VI of ♂ with 1 or 2 pairs of ambulatory setae.

Male genitalia. Median lobe lacking apical disc.

Female genitalia. Valvifer moderately sclerotized, varied in shape. Stylus with apical segment moderately to strongly elongate. Proctiger well sclerotized, distal portion free from tergum in many species.

*Discussion.* — The genus *Progonochaetus* is a well defined group possessing the apomorphic character states of: paraglossa with at least some setae on dorsal base and usually also elsewhere; pronotum with 2 lateral setae on each side; and apical segment of female stylus elongate.

The species of *Progonochaetus* comprise 2 groups based primarily on pronotal form. The first group is the nominate subgenus and includes those species in which the pronotum (Figs. 184, 186) is semirectangular in form, has a non-sinuate side, and non-projected posterior angle. The second group is the subgenus *Eudichirus* containing those species in which the pronotum (Fig. 187) is semicordate with the side sinuate before the outward projected posterior angle. The nominate subgenus contains those species included in *Progonochaetus* by Basilewsky (1950), all species formerly included by him in *Dichaetochilus* and *Oligoxemus*, and a single Oriental species formerly placed in the genus *Pseudognathaphanus*. The subgenus *Eudichirus* includes those species formerly included in *Eudichirus* and *Rasnodactylus* by Basilewsky (1950).

*Progonochaetus* was treated by Basilewsky (1950) as a monotypic genus containing only the species *xanthopus*. The paraglossa of *xanthopus* has long prominent seta along its mesal margins and on its dorsal base. Species of *Dichaetochilus*, *Oligoxemus*, *Rasnodactylus*, and *Eudichirus* were stated to have glabrous paraglossa and therefore to belong to different genera than *xanthopus*. However, dissection of specimens of these former 4 genera reveals that all their species have setae on the dorsal base and often also on the mesal margins of the paraglossa. These setae vary in number, length, thickness, and location according to the species being examined. The species *xanthopus* is merely a species in which the setae are especially long and numerous; its characters do not require that it be given separate generic status.

Basilewsky (1950) distinguished *Oligoxemus* from *Dichaetochilus* by possession of 2, rather than 1, setae at each outer distal angle of the clypeus. This single character is not sufficient to warrant separate generic or subgeneric status in view of the inter- and intra-specific variation shown by this character in *Anisodactylus*. Since the species of *Oligoxemus* and *Dichaetochilus* differ in no significant characters from *xanthopus*, both genera must be combined with *Progonochaetus*.

Basilewsky (1950) distinguished *Rasnodactylus* from other Anisodactylina genera due to its single species, *jeanneli*, possessing an unmodified male midtarsus (that is, not laterally expanded and not spongy pubescent beneath). However the state of the male midtarsus is not a reliable intergeneric character within Anisodactylina. For example, in the subspecies *Dicheirus dilatatus angulatus* the male midtarsus varies from unmodified to laterally expanded and spongy pubescent beneath (Noonan, 1968). The former genus *Eudichirus* was regarded as containing the species *ochropus* and *pseudochropus*. However, in both of these species the segments of male midtarsus are at most only very slightly expanded laterally and each bear only a relatively small patch of spongy pubescent vestiture. I have seen one male of *pseudochropus* in which the male midtarsus is completely unmodified. There is not sufficient

reason to keep separate the species of the former genera *Eudichirus* and *Rasnodactylus*.

The species *Dichaetochilus jeanneli* Basilewsky, 1946 and *Rasnodactylus jeanneli* Basilewsky, 1946 are now both members of the genus *Progonochaetus*. I here propose "*basilewskyi*" as a replacement name for the former species.

14 subgenus *Progonochaetus* G. Müller  
(Figs. 184, 186)

*Progonochaetus* G. Müller, 1938: 245. [TYPE SPECIES: *Anisodactylus xanthopus* Dejean, 1829, by original designation].

*Dichaetochilus* Basilewsky, 1946 a: 7. [TYPE SPECIES: *Selenophorus aeruginosus* Dejean, 1829, by original designation. NEW SYNONYMY].

*Oligoxemus* Basilewsky, 1948: 66. [TYPE SPECIES: *Anisodactylus limbatus* Quedenfeldt, 1883, by original designation and monotypy. NEW SYNONYMY].

*Description.*

Thorax. Pronotum (Figs. 184, 186) semirectangular, somewhat transverse; side not sinuate; posterior angle not outward projected.

Legs. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with segments II to IV laterally expanded and spongy pubescent beneath.

*Discussion.* — This subgenus contains 1 Oriental species and 38 Ethiopian ones. The single Oriental species, *laevistriatus* (Sturm), 1918, is found in India and Bruma. It was formerly placed in the genus *Pseudognathaphanus*. However in *laevistriatus*: the mentum and submentum are separated by a transverse suture which appears complete in some specimens, narrowed and vestigial laterally in others, and present medially but absent laterally in others; there are 2 pronotal lateral setae; the paraglossa has dorsal setae; and the apical segment of the female stylus is elongate.

The 38 Ethiopian species are found in Africa south of the Sahara and in Madagascar and are: *aeruginosis* (Dejean), 1829\*; *angolanus* (Basilewsky), 1946; *approximatus* (Kolbe), 1897; *arnoldi* (Basilewsky), 1948; *atrofuscus* (Fairmaire), 1869\*; *bamboutensis* (Basilewsky), 1948\*; *basilewskyi*, *nomen novum* for *Dichaetochilus jeanneli* Basilewsky, 1946; *bicoloripes* (Burgeon), 1936; *brittoni* (Basilewsky), 1946; *caffer* (Boheman), 1848; *chevalieri* (Basilewsky), 1946\*; *colnanti* (Burgeon), 1936; *cursorius* (Basilewsky), 1946; *decorsei* (Basilewsky), 1948\*; *dilatatus* (Klug), 1853\*; *discrepans* (Basilewsky), 1946; *emarginatus* (Dejean), 1829; *inchoatus* (Peringuey), 1908\*; *incrassatus* (Boheman), 1848\*; *kafakumbae* (Basilewsky), 1949\*; *kapangae* (Burgeon), 1936; *laeticolor* (Chaudoir), 1876\*; *limbatus* (Quendenfeldt), 1883; *longesulcatus* (Basilewsky), 1949\*; *merus* (Basilewsky), 1949\*; *moestus* (Chaudoir), 1878; *nigricrus* (Dejean), 1828\*; *obtusius* (Basilewsky), 1946; *piceus* (Dejean), 1829\*; *planicollis* (Putzeys), 1880; *prolixus* (Basilewsky), 1948\*; *rudebecki* (Basilewsky), 1946\*; *sakalava* (Jeannel), 1948\*; *seyrigi* (Jeannel), 1948\*; *straneoi* (Basilewsky), 1949\*; *subcupreus* (Chaudoir), 1876; *vagans* (Dejean), 1831\*; *xanthopus* (Dejean), 1829.

The 38 Ethiopian species can be distinguished by means of the generic and specific keys provided by Basilewsky (1950). The single Oriental species can be distinguished on the basis of its geographical distribution.

15 subgenus *Eudichirus* Jeannel NEW STATUS

(Fig. 187)

*Eudichirus* Jeannel, 1946: 158. [TYPE SPECIES: *Anisodactylus ochropus* Dejean, 1948, by original designation].

*Rasnodactylus* Basilewsky, 1946 b: 17. [TYPE SPECIES: *Rasnodactylus jeanneli* Basilewsky, 1946, by original designation. NEW SYNONYMY].

*Description.*

Thorax. Pronotum (Fig. 187) semicordate, with side sinuate before the pointed outward projected posterior angle.

Legs. Foretarsus of ♂ with some segments slightly expanded laterally and in some specimens spongy pubescent beneath. Midtarsus of ♂ unmodified in *jeanneli*, but in most specimens of other species with some segments slightly expanded laterally and spongy pubescent beneath.

*Discussion.* — The subgenus *Eudichirus* contains 3 very similar appearing named species which all occur in Africa: *jeanneli* (Basilewsky), 1946; *ochropus* (Dejean), 1829 ♀\*; and *pseudochropus* (Kuntzen), 1919 ♀\*. It is possible that the last 2 forms may be conspecific. The 3 species can be separated by using the generic and specific keys provided by Basilewsky (1950).

16 genus *Phanagnathus* Basilewsky

*Phanagnathus* Basilewsky, 1950: 35. [TYPE SPECIES: *Anisodactylus overlaeti* Burgeon, 1936, by monotypy and original designation].

*Description.* — Body length 9 to 10 mm. Body relatively stout.

Color. Body dark piceous to black.

Head. Labral apex moderately emarginate medially. Frons with fovea obsolescent, bearing weak clypeo-ocular prolongation; microsculpture obsolescent. Eye large and protruding. Gena narrow, width at narrowest point less than maximum width of first antennal segment. Mentum with moderately prominent tooth. Mentum and submentum completely fused. Submentum with 1 long seta on each side. Ligula narrow, slightly expanded laterally at apex. Paraglossa slightly longer than ligula.

Thorax. Pronotum transverse, constricted basally; lateral depression obsolescent; lateral bead complete; basal and apical beads present laterally; microsculpture obsolete in ♂, consisting of weak transverse mesh in ♀.

Legs. Foretibia with distal portion moderately expanded laterally; apical spur lanceolate. Hindfemur of most specimens with 2 long setae on posterior margin. Hindtarsus with segment I longer than II + III. Dorsum of all tarsi irregularly pubescent. Fore- and midtarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Scutellar stria short; intervals flat to slightly convex basally but more convex apically; interval III with several dorsal setigerous punctures apically; interval VII with distal ocellate puncture; subapical sinuation slight; microsculpture obsolescent in ♂, consisting of weak transverse mesh in ♂.

Abdomen. Sternum VI of ♂ with 2 pairs of ambulatory setae. Tergum VIII of ♀ with apex obtusely angulate.

Male genitalia. Median lobe lacking apical disc.

Female genitalia. Valvifer slightly convex, moderately sclerotized, with several distal setae; distal mesal and lateral margins somewhat membranous.

*Discussion.* — This genus contains the single species *overlaeti* (Burgeon), 1936 which is found in the Belgian Congo.

### 17 genus *Pseudognathaphanus* Schauberger

*Pseudognathaphanus* Schauberger, 1932: 57. [TYPE SPECIES: *Harpalus punctilabris* MacLeay, 1825, by original designation].

*Protognathus* Basilevsky, 1950: 36. [TYPE SPECIES: *Anisodactylus zabroides* Alluaud, 1917, by original designation. NEW SYNONYMY].

*Description.* — Body length 9 to 15 mm. Body elongate, moderately convex.

Color. Body brown to black, no metallic tinge.

Head. Labral apex straight to slightly emarginate medially. Clypeal apex straight to moderately emarginate medially. Frontal fovea moderate, bearing prominent clypeo-ocular prolongation. Mentum lacking tooth. Mentum and submentum completely fused. Ligula narrow, not expanded laterally at apex. Paraglossa longer than ligula.

Thorax. Pronotum with lateral bead complete; apical and basal beads present at least laterally.

Legs. Foretibia with distal portion moderately expanded laterally; apical spur lanceolate to swollen basally. Hindfemur of most specimens with 2 long setae on posterior margin. Hindtarsus with first segment approximately 2.5 to 3 times as long as wide at apex, shorter than II + III. Segments II to IV of hindtarsus of both sexes and segments II to IV of fore- and midtarsus of ♀ with dense ventro-lateral cover of somewhat thickened setae. Fore- and midtarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Intervals flat to slightly convex; specimens of *dekannus* with only 1 dorsal setigerous puncture, this puncture located near apical 1/5 of interval III, specimens of other species with several to many dorsal setigerous punctures located on various intervals; interval VII with minute ocellate puncture at extreme apex and large prominent ocellate puncture slightly more proximal.

Hind wing. Full and probably functional in all species examined.

Abdomen. Sternum VI with 1 or 2 pairs of ambulatory setae in ♂.

Male genitalia. Median lobe with or without apical disc.

Female genitalia. Valvifer various depending on species.

Jedlička (1957) treated *Pseudognathaphanus* (*s. str.*) as a subgenus of the genus *Kareya* Andrewes, 1919 because of the similar body shape of species of these groups. The description provided by Andrewes for the genus *Kareya* and the comments of Jedlicka (1957) make it apparent that the genus *Kareya* does not belong to the subtribe Anisodactylina. Therefore, the treatment proposed by Jedlicka (1957) is not accepted here.

The genus *Pseudognathaphanus* contains 6 species in the Oriental Region and 2 in Madagascar. The latter 2 species previously constituted the genus *Protognathus*, but no constant morphological characters warrant separate generic status for *Pseudognathaphanus* and *Protognathus*. And the species of these 2 groups are characterized by the apomorphic feature of segments II to IV of the hindtarsus of both sexes and segments II to IV of fore- and midtarsus of females with a dense ventro-lateral cover of somewhat thickened setae.

The 6 Oriental Region species of *Pseudognathaphanus* are found in India, Ceylon, Burma, and Indochina except for the widespread species *punctilabris* which also occurs in China, Formosa, and Philippine Islands, Java, and Sumatra. These species are: *dekkanus* Andrewes, 1933; *exaratus* (Bates), 1892; *festivus* (Andrewes), 1921 ♂; *punctilabris* (MacLeay), 1825; *rufitactor* (Bates), 1892\*; *rusticus* (Andrewes), 1920. The 2 species on Madagascar are:



*perrieri* (Jeannel), 1948\*; and *zabroides* (Alluaud), 1917. The species of the Oriental Region may be identified by the key in Jedlicka (1957). The 2 species found on Madagascar may be distinguished by the keys in Basilewsky (1950).

18 genus *Chydaeus* Chaudoir  
(Fig. 172)

*Chydaeus* Chaudoir, 1854: 343. [TYPE SPECIES: *Chydaeus obscurus* Chaudoir, 1854, by monotypy].

*Acrogeniodon* Tschitscherine, 1897: 65. [TYPE SPECIES: *Acrogeniodon bedeli* Tschitscherine, 1897, by monotypy].

*Hayekius* Habu, 1955: 35. [TYPE SPECIES: *Ophonus constrictus* Bates, 1833, by monotypy].

*Description.* — Body length approximately 9 to 14 mm. Body narrow, but in some specimens appearing stout due to broad elytra.

Color. Body dark piceous to black.

Head. Labral apex strongly emarginate medially. Frontal fovea obsolescent to moderately prominent and punctiform or somewhat linear, with or without clypeo-ocular prolongation. Mentum with very prominent, long tooth (Fig. 172). Mentum and submentum completely fused. Ligula narrow or moderately expanded at apex. Paraglossa slightly longer than ligula and well removed distally from it.

Thorax. Pronotum relatively small, somewhat cordate; lateral bead complete; basal bead complete in most specimens, but obsolescent medially in some specimens. Apical bead present laterally.

Legs. Foretibia with distal portion moderately expanded laterally; apical spur lanceolate. Hindfemur of most specimens with 2 long setae on posterior margin. Hindtarsus with segment I slightly shorter to slightly longer than II + III. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Scutellar stria with length varied within individual species, in many specimens distal portion of stria I captured and base of stria I left as apparent false scutellar stria (see discussion); intervals flat to convex, no setigerous punctures; interval VII with distal ocellate puncture.

Abdomen. Sternum VI of ♂ with 2 pairs of ambulatory setae. Tergum VIII of ♀ with rounded apex.

Male genitalia. Median lobe lacking apical disc.

Female genitalia. Valvifer slightly convex, moderately sclerotized, with several distal setae; distal mesal margin somewhat membranous and without discrete boundary. Proctiger modified into moderately sclerotized elongate plate on each side of anal orifice and with or without setae.

*Discussion.* — Tschitscherine (1897), who apparently never saw identified specimens of *Chydaeus*, described the monobasic *Acrogeniodon*. Andrewes (1919) treated it as congeneric with *Chydaeus*, and subsequent authors have accepted this treatment.

Habu (1955) and Tanaka (1958) accorded the species *constrictus* separate generic status in the monotypic genus *Hayekius*. Habu (1973) treated *Hayekius* as congeneric with *Chydaeus* but did not give reasons for this treatment. Habu (1955) and Tanaka (1958) originally felt *Hayekius* warranted separate generic status because its sole species, *constrictus*, was stated to have the scutellar stria originating on the first elytral interval and the metepisternum not longer than wide. But the holotype of *constrictus* has an unmodified scutellar

stria arising from an ocellate puncture at the base of stria II; and considerable variation of the scutellar stria occurs in *constrictus*, *bakeri* and probably other species of *Chydaeus*. The scutellar stria in specimens of *constrictus* and *bakeri* can be: (1) unmodified; (2) elongate, curved distally towards stria I; (3) elongate, joining stria I distally; (4) elongate, completely capturing the distal portion of stria I, with basal portion of stria I nearly reaching point of juncture; (5) elongate, completely capturing the distal portion of stria I, basal portion of stria I short and appearing on first glance to be the scutellar stria. The length of the metepisternum varies depending on whether the hind wings are functional or vestigial.

Schauberger (1934) provided a key to the species known at that time, and Habu (1973) provided a fine key to the species found in Japan. Additional species have been described since Schauberger's revision, and *Chydaeus* is in need of revision.

Species of the genus are concentrated in southern China, northern India, Tibet, and Sikkim but some occur as far towards Australia as New Guinea. The 20 named species are: *andrewesi* Schauberger, 1932; *bakeri* Andrewes, 1926; *bedeli* (Tschitscherine), 1897; *constrictus* (Bates), 1883; *formosanus* Tanaka, 1958\*; *gestroi* Andrewes, 1929; *hinus* Darlington, 1971\*; *javanicus* Schauberger, 1932; *jedlickai* Schauberger, 1934\*; *kirishimanus* Habu, 1973\*; *miwai* Jedlicka, 1946\*; *obscurus* Chaudoir, 1854; *obtuscollis* Schauberger, 1932; *papua* Darlington, 1968; *planicollis* Andrewes, 1931; *rufipes* Jedlicka, 1940\*; *schaubergeri* Jedlicka, 1931; *shibatai* Habu, 1973\*; *shikokuensis* Habu, 1973\*; and *yunnanus* Jedlicka, 1940\*. Darlington (1968) mentioned that many of the species are restricted to mountainous areas.

#### 19 genus *Harpalomimetes* Schauberger

*Harpalomimetes* Schauberger, 1933: 133. [TYPE SPECIES: *Anisodactylus sjostedti* Andrewes, 1926, by original designation].

*Description.* — Body slender, dorsal microsculpture obsolescent or absent, dorsum covered with fine non-setigerous punctures.

*Color.* Body black. Elytron iridescent.

*Head.* Rather large with broad neck. Labral apex moderately emarginate medially. Clypeal apex moderately emarginate medially. Frontal fovea punctiform, with fine but discernible clypeo-ocular prolongation. Mentum without tooth. Mentum and submentum completely fused. Ligula narrow, slightly expanded laterally at apex. Paraglossa slightly longer than ligula, separated distally from it.

*Thorax.* Pronotum suborbiculate; lateral bead complete; apical and basal beads present at least laterally; sides and lateral portions of base and apex with small dense non-setigerous punctures.

*Legs.* Foretibia with distal portion moderately expanded laterally; apical spur lanceolate. Hindtarsus with segment I shorter than II + III. Fore- and midtarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath.

*Elytron.* Intervals slightly to moderately convex and iridescent, more so in ♂; interval III with dorsal setigerous puncture near apical 1/3; interval VII with apical ocellate puncture; microsculpture absent.

*Abdomen.* Sternum VI of ♂ with 2 pairs of ambulatory setae.

*Male genitalia.* Median lobe with very small apical disc.

*Female genitalia.* Valvifer moderately sclerotized, subtriangular in shape, with several distal setae.

*Discussion.* — This genus contains the 2 species: *sjostedti* (Andrewes), 1926 found in Sumatra and the Philippines; and *andrewesi* Schauberger, 1933 found in Indochina and

Japan. I have not examined specimens of *andrewesi*. Tanaka (1958) redescribed that latter species, and I have relied on this redescription in preparing the generic description.

## 20 genus *Rhysopus* Andrewes

*Rhysopus* Andrewes, 1929: 358. [TYPE SPECIES: *Rhysopus klynstrai* Andrewes, 1929, by monotypy].

*Description.* — Body length 11 to 12 mm.

Color. Body black; shiny and faintly iridescent due to reduced microsculpture.

Head. Large with broad neck. Labral apex strongly emarginate medially. Clypeal apex moderately emarginate medially. Frontoclypeal suture extremely deep, extended laterally to region of frontal fovea then postero-laterally toward eye as very deep clypeo-ocular prolongation. Frontal fovea obliterated by the very deep frontoclypeal suture. Mentum completely fused to submentum and lacking tooth or setae. Ligula strongly expanded laterally at apex. Paraglossa slightly longer than ligula, separated distally from it.

Thorax. Pronotum widest just before middle, sides thence convergent towards base; posterior angle broadly rounded; side and lateral portion of base with coarse non-setigerous punctures and lateral portion of apex with smaller non-setigerous punctures; lateral bead complete; apical and basal beads present laterally and in most specimens also medially.

Legs. Foretibia with distal portion moderately expanded laterally; apical spur trifid. Hindfemur with 2 long setae on posterior margin. Hindtarsus with segment I = to II + III in most specimens. Fore- and midtarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Intervals convex and with numerous small non-setigerous punctures; interval III with dorsal setigerous puncture about 1/3 from apex; interval VII with apical ocellate puncture; stria deep and wide; subapical sinuation moderate; microsculpture of extremely fine transverse lines.

Abdomen. Sternum VI of ♂ with 2 pairs of ambulatory setae. Tergum VIII of ♀ with rounded apex.

Male genitalia. Median lobe without apical disc.

Female genitalia. Valvifer moderately sclerotized, apical portion becoming narrower and blade like distally and with several distal setae.

*Discussion.* — *Rhysopus* includes only the single species *klynstrai* Andrewes, 1929 found in Java, Sumatra, and the Tonkin area of Indochina. In describing this genus, Andrewes emphasized the male fore- and midtarsi which he reported to have on the underside of the expanded segments "12 to 15 fine longitudinal ridges, and twice as many scales, transversely placed between each two adjacent ridges". Actually the ridges are merely the basal portions of the setae which distally form the spongy pubescence found in Anisodactylines, and the male tarsi thus are not different from those found in other Anisodactylines. However *klynstrai* warrants separate generic status due to the extremely deep frontoclypeal suture and the elytral microsculpture of extremely fine transverse lines.

## 21 genus *Xestonotus* LeConte

(Figs. 173, 212, 213, 227)

*Xestonotus* LeConte, 1853: 383. [TYPE SPECIES: *Selenophorus lugubris* Dejean, 1829, by monotypy].

*Description.* — Body length 9.2 to 11.0 mm. Body relatively slender with large head and small eyes.

Color. Body rather dull black.

Head. Frontal fovea punctiform, small. Mentum without tooth. Mentum and submentum completely fused. Ligula (Fig. 173) not expanded laterally at apex; moderately to strongly laterally expanded subapically. Paraglossa (Fig. 173) subequal to or slightly longer than ligula; apex obtuse.

Thorax. Pronotum broad with all angles rounded; lateral bead fine but complete; apical and basal beads present, flattened and obsolete medially in most specimens; microsculpture of slightly transverse isodiametric mesh, more prominent in ♀. Prosternum sparsely pubescent. Proepisternum, mesepisternum, mesepimeron, metepisternum, metepimeron glabrous. Mesosternum pubescent. Metasternum sparsely pubescent near midcoxa and in some specimens near midline.

Legs. Foretibia with distal portion slightly expanded laterally; apex emarginate, outer angle of emargination rounded; apical spur lanceolate. Hindtarsus with segment I = to II + III in most specimens. Dorsum of all tarsi sparsely pubescent. Foretarsus of ♂ with segments I to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Interval III of most specimens with dorsal setigerous puncture adjacent to stria II on apical 1/3; microsculpture of slightly irregular and slightly granulate isodiametric mesh, more prominent in ♀.

Abdomen. Sternum VI of ♂ with 2 pairs of ambulatory setae. Tergum VIII of ♀ with apex rounded.

Male genitalia. Median lobe (Figs. 212, 213) strongly asymmetrical, swollen medially; apex bent ventrad; right latero-ventral margin with small serrations. Internal sac in repose with prominent spine inserted on scaly field protruded through ostium; everted sac with 2 prominent spines, one apical and with small scaly field at base, other basal (one which protrudes from ostium when sac in repose) and with scaly field extended distally from it.

Female genitalia. Valvifer (Fig. 227) flattened, moderately sclerotized, with varied number of distal setae.

*Discussion.* — This genus contains only the species *lugubris* (Dejean), 1829 found in southeastern Canada and the eastern United States. Past workers have treated *Xestonotus* as a separate genus or included it in *Anisodactylus*. Although Lindroth (1968) treated it as a subgenus of *Anisodactylus* because he found no external characters to warrant generic separation, he did so reluctantly because of the very different and highly asymmetrical median lobe of *lugubris*. However the ligula of *lugubris* differs from that of all species of *Anisodactylus*, and *lugubris* is accorded separate generic status.

## 22-31 genus *Anisodactylus* Dejean

*Anisodactylus* Dejean, 1829: 132. [TYPE SPECIES: *Carabus binotatus* Fabricius, 1787, designated by Westwood (1838)].

*Description.* — Body length 7.0 to 19 mm. Body stout and *Amara*-like to cylindrical and convex.

Color. Various.

Head. Clypeus with 1 to several setigerous punctures at each outer angle. Frons with fovea various but in most specimens with clypeo-ocular prolongation; microsculpture in most species of isodiametric mesh, obsolescent medially in some species, of granulate isodiametric mesh or of punctures in a few species. Mentum without tooth or with small tooth. Mentum and submentum completely fused. Ligula strongly expanded laterally at apex, or only moderately expanded in specimens of *californicus*, *furvus*, and *kirbyi*. Paraglossa membranous,

slightly longer than ligula.

Thorax. Pronotum with lateral, apical, and basal beads present; microsculpture of isodiametric mesh, or granulate isodiametric mesh, of punctures, or obsolete.

Elytron. Outer intervals, base, and apex pubescent in some species; inner intervals not densely and regularly pubescent.

Abdomen. Sternum VI of ♂ with 1 or 2 pairs of ambulatory setae.

Male genitalia. Median lobe arcuate except in subgenus *Pseudhexatrichus*; with or without apical disc. Internal sac with or without armature.

Female genitalia. Valvifer various, constant in shape for species of most subgenera.

*Discussion.* — This is the largest genus in the subtribe and contains 10 subgenera and 54 species. The genus is found in North America, Europe to tropical Asia, areas adjacent to the Mediterranean, northern Africa, Japan, Korea, India, Burma, and Indochina.

Authors have had differing opinions as to the exact composition of the genus. These opinions are reviewed under the 10 subgenera recognized here.

Information on the identification of specimens is also presented in the discussion section for each subgenus.

I have not determined the proper subgeneric placement of 7 species of which I have not seen examples and of which I can not gain sufficient information from the literature. These 7 species are: *abaculus* Bates, 1889, described from Liberia; *amplicollis* Gerstaecker, 1867, described from east Africa; *mandschuricus* Jedlicka, 1924, described from Manchuria, China; *metallescens* Putzeys, 1880, described from Angola; *obscuripes* LaFerté, 1853, described from Africa; *obtusicollis* Putzeys, 1880, described from Angola; and *schaubergi* Jedlicka, 1932, described from Yunnan, China. The 5 species from Africa may belong to genera other than *Anisodactylus*.

## 22 subgenus *Anisodactylus* Dejean

(Figs. 198, 217, 218)

*Anisodactylus* Dejean, 1829: 132. [TYPE SPECIES: *Carabus binotatus* Fabricius, 1787, designated by Westwood (1838)].

*Cephalogyna* Casey, 1918: 414. [TYPE SPECIES: *Anisodactylus lodingi* Schaeffer, 1911, by monotypy].

*Description.* — Body length approximately 7 to 19 mm. Body convex, with pronotum small and elytra elongate and subparallel.

Color. Body color unmetallic piceous to black. Frons except for occasional specimens in some species, with double more or less confluent rufous spot medially.

Head. Labral apex straight to strongly emarginate medially. Clypeus with apex straight to moderately emarginate medially; species of the Old World with 1 setigerous puncture at each outer distal angle; species of the New World with 1 to several (number varied within many species) setigerous punctures at each outer distal angle. Frontal fovea various, in most specimens with more or less evident clypeo-ocular prolongation, also in many specimens with medially directed prolongation producing a somewhat Y shaped fovea. Mentum without a tooth or with small tooth in some specimens of various North American species. Paraglossa slightly longer than ligula.

Thorax. Shape and form of pronotum various. Prosternum of most specimens pubescent at sides; glabrous or pubescent medially.

Legs. Foretibia with distal portion moderately expanded laterally; apical spur dilated near base, varied within several species from evenly dilated and non angulate to strongly angulate or even subtrifid (as in most specimens of *similis*), clearly trifid in *carbonarius*, *tricuspidatus*,

and *karennius*. Hindfemur with 2 long setae, or in specimens of *carbonarius*, *similis*, *signatus*, and *binotatus* with 2 to 5 such setae. Hindtarsus with segment I = to or longer than II + III in all species but *signatus*, *tricuspidatus*, *nemorivagus* and *karennius*. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with apex of segment I in some specimens and all of segments II to IV in all specimens laterally expanded and spongy pubescent beneath.

Elytron. Humerus rounded to angulate depending on species; outer intervals, base, and apex pubescent in some species; intervals flat to convex; interval III with single dorsal setigerous puncture, such puncture lacking in *signatus*, and *tricuspidatus* with 1 to 2 such punctures; intervals II and V of some specimens with 1 or more distal setigerous punctures; interval VII with distal ocellate puncture and in some specimens with 1 or more distal setigerous punctures; intervals of some specimens covered with non-setigerous punctures.

Hind wing. Full and apparently functional in all species except *agricola*.

Abdomen. Sternum VI of ♂ with 1 pair of ambulatory setae in most species. Apex of tergum VIII of ♀ broadly rounded (Fig. 198).

Male genitalia. Median lobe with apex symmetrical and lacking disc; shaft twisted in *binotatus*; membranous portion of dorsum various in size and extension towards basal bulb, nearly reaching basal bulb in several species, in *similis* reaching basal bulb and occupying most of dorsum distal to it, divided into 2 parts in *binotatus*. Internal sac with or without armature.

Female genitalia. Valvifer strongly sclerotized; distal portion triangular in shape and with setae of various numbers and sizes (Figs. 217, 218).

*Discussion.* — This is the most widespread subgenus of the subtribe and is represented in temperate North America, Europe to China, Japan, Korea, Burma, and Africa north of the Sahara Desert. It was formerly thought to also be present in tropical Africa, but Basilewsky (1950) demonstrated that the species there belong to a different genera.

The North American forms are well understood since Lindroth (1968) completed an excellent revision and provided a key to them. Puel (1931) provided a usable key to species of the Palearctic region, Jeannel (1942) keyed out those of France, and Tanaka (1958) provided good keys to those of Japan and in part to those of Korea and China. And Habu (1973) provided fine keys to the species of Japan.

The only species not treated in one of the above works are *karennius* (Bates), 1892 and *pueli* Schauburger, 1933. The species *karennius* is found in India, Burma, and Indochina. Csiki (1932) listed *hauseri* Schauburger as being conspecific with *karennius*. However, Puel (1931) cited *hauseri* as having a simple foretibial apical spur while the foretibial apical spur in the 7 specimens I have seen of *karennius* are trifid. The only other Palearctic species possessing a trifid foretibial apical spur is *tricuspidatus*. The species *karennius* and *tricuspidatus* are distinguished from each other by elytron of *karennius* glabrous except for a dorsal puncture on interval III and an apical ocellate puncture on interval VII, and elytral intervals of *tricuspidatus* densely covered with non-setigerous punctures. The species *pueli* is recorded from Albania to Turkey; I have seen only 1 female specimen of it and can not provide information on distinguishing this form from other species.

I have seen males and females of all 13 North American species. These species are: *agricola* (Say), 1823; *binotatus* (Fabricius), 1787 (introduced from Eurasia); *californicus* Dejean, 1829; *carbonarius* (Say), 1823; *consobrinus* LeConte, 1851; *furvus* LeConte, 1863; *harrisi* LeConte, 1863; *loedingi* Schaeffer, 1911; *kirbyi* Lindroth, 1953; *melanopus* Halde-  
man, 1843; *nigerrimus* (Dejean), 1831; *nigrita* Dejean, 1829; and *similis* LeConte, 1851.

Casey (1918) proposed a separate genus, *Cephalogyna*, for the species *loedingi*. Lindroth (1968) quite correctly regarded *Cephalogyna* as congeneric with the subgenus *Anisodactylus*.

While *loedingi* is the largest species in the subgenus, and in fact in the genus, it has the type of female valvifer and female abdominal tergum VIII diagnostic for the subgenus *Anisodactylus*.

The species *carbonarius* was formerly treated as a member of the subgenus *Gynandrotarsus* because of its trifid foretibial apical spur. However, this character is not diagnostic as formerly believed. The Old World species *tricuspидatus* and *karennius* also have trifid foretibial spurs, and several North American species have swellings or are slightly angulate at each side of their spurs. Lindroth (1968) pointed out that *carbonarius* has the general habitus (more slender than that of *Gynandrotarsus*) of species of the subgenus *Anisodactylus* and has pubescence medially on the prosternum. "True" *Gynandrotarsus* have the prosternum glabrous medially, possess the type of female valvifer described for that subgenus, and have the apex of the female abdominal tergum VIII angulate. Instead *carbonarius* has the type of female valvifer and the apically more rounded female abdominal tergum VIII found in all members of the subgenus *Anisodactylus*, and I am here transferring *carbonarius* to this taxon.

The 12 species found in the Old World are: *antoinei* Puel, 1931\*; *atricornis* (Stephens), 1835\*; *binotatus* (Fabricius), 1787; *hauseri* Schauburger, 1931\*; *hispanus* Puel, 1931 ♀\*; *karennius* (Bates), 1892; *nemorivagus* Duftschmidt, 1812; *nigricornis* (Stephens), 1835\*; *propinquus* Ballion, 1870\*; *shibatai* Habu, 1969\*; *signatus* (Panzer), 1797; and *tricuspидatus* Morawitz, 1863.

The species *sadoensis* Schauburger, 1931 and *punctatipennis* Morawitz, 1862 formerly considered members of this subgenus have been removed to a new subgenus, *Pseudanisodactylus*, for reasons discussed under that taxon.

Jeannel (1942) treated the subgenus *Pseudodichirus* with its single species *intermedius* Dejean, 1829 as congeneric with the subgenus *Anisodactylus*. For reasons discussed under the subgenus *Pseudodichirus*, I have revalidated this subgenus and transferred *intermedius* back to it.

### 23 *Pseudanisodactylus* NEW SUBGENUS

(Fig. 221)

TYPE SPECIES: *Anisodactylus punctatipennis* Morawitz, 1862, here designated.

*Description.* — Body length 9.5 to 13.5 mm. Body form as in nominate subgenus; entire dorsum densely covered with small non-setigerous punctures.

Color. Body dark piceous to black. Head with frons bearing median rufous spot.

Head. Labral apex moderately to strongly emarginate medially. Clypeal apex straight to moderately emarginate medially. Frontal fovea Y shaped, one arm forming clypeo-ocular prolongation, other arm directed medially. Paraglossa slightly longer than ligula.

Thorax. Pronotum cordiform. Prosternum densely pubescent. Proepisternum pubescent anteriorly, remainder without pubescence but covered with non-setigerous punctures. Propimeron, mesepisternum, mesepimeron, metepisternum, metepimeron covered with non-setigerous punctures but lacking pubescence in most specimens. Meso- and metasternum pubescent.

Legs. Foretibia with distal portion moderately expanded laterally; apex weakly emarginate in ♂, more prominently emarginate in ♀; apical spur obtusely dilated near middle. Hindtarsus relatively slender; segment I = to II + III in most specimens. Dorsum of all tarsi densely pubescent.

Elytron. Apex and base of intervals I to VII, all of intervals VIII to X pubescent; interval III without dorsal setigerous puncture.

Abdomen. Sternum VI with 1 pair of ambulatory setae in ♂. Abdominal tergum VIII of ♀ as in nominate subgenus (Fig. 198).

Male genitalia. Median lobe lacking apical disc.

Female genitalia. Valvifer (Fig. 221) moderately sclerotized, slightly convex, lobed; with several distal setae of various numbers, sizes and arrangements.

*Discussion.* — This new subgenus contains the species *punctatipennis* Morawitz, 1862 found in Japan, Korea, and China, and the species *sadoensis* Schaubberger, 1931 found in Japan. These 2 species were formerly placed in the subgenus *Anisodactylus* but differ from all species of that subgenus by valvifer lobed, nontriangular. The species *punctatipennis* and *sadoensis* are distinguished from other Asian species of *Anisodactylus* by the key in Tanaka (1958).

*Derivation of name.* — The name "*Pseudanisodactylus*" refers to the close external resemblance of included species to those of the subgenus *Anisodactylus*.

#### 24 subgenus *Pseudhexatrachus* NEW SUBGENUS

(Figs. 191, 214, 215, 219)

*Pseudhexatrachus* Puel, 1931: 61. [NOMEN NUDUM (see discussion) TYPE SPECIES: *Anisodactylus dejeani* Buquet, 1840, here designated].

*Description.* — Body length 9.5 to 12.5 mm. Body form as in nominate subgenus.

Color. Dorsum bicolored; head rufotestaceous; pronotum bluish black; elytron rufotestaceous basally, bluish black medially and apically.

Head. Labral apex slightly to moderately emarginate medially. Clypeal apex straight to slightly emarginate medially. Frontal fovea with clypeo-ocular impression, in some specimens also with medially directed linear impression. Mentum without or with vestigial tooth. Paraglossa slightly longer than ligula.

Thorax. Pronotum constricted basally; pubescent near anterior angle. Prosternum pubescent except for median glabrous area. Proepisternum pubescent anteriorly, glabrous elsewhere. Remainder of venter pubescent.

Legs. Hindfemur with 2 long setae on posterior margin. Foretibia with inner basal margin broadly emarginate in ♂ (Fig. 191), unmodified in ♀; apical spur dilated medially but not clearly angulate; apex with brief emargination near outer angle. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with segments II to IV laterally expanded and spongy pubescent beneath. Hindtarsus relatively slender; segment I = to or slightly shorter than II + III.

Elytron. Interval III of most specimens with 2 dorsal setigerous punctures on apical 1/3 (a few specimens with 1 or 3 such punctures); interval VII with 2 to 6 apical setigerous punctures.

Abdomen. Sternum VI of ♂ with 1 pair of ambulatory setae. Apex of tergum VIII of ♀ obtusely rounded.

Male genitalia. Median lobe (Figs. 214, 215) with shaft only very slightly arcuate and with distal portion asymmetric and bent to right.

Female genitalia. Valvifer (Fig. 219) as in nominate subgenus. Stylus with apical segment slightly compressed latero-medially.

*Discussion.* — This subgenus contains 2 species: *heros* (Fabricius), 1801 from Portugal, Spain, Sardinia, Algeria, and Morocco; and *dejeani* Buquet, 1840 from Algeria, Tunisia, and Sardinia. The 2 species are identified in the key provided by Puel (1931).

In his key to the Palearctic species of *Anisodactylus*, Puel (1931) assigned the subgeneric name "*Pseudhexatrachus*" to these species. However he did not designate a type species for the subgenus, and the subgeneric name proposed by him must therefore be regarded as a



*nomen nudum* according to the provisions of article 13b of the International Code of Zoological Nomenclature. For reasons outlined below I feel *heros* and *dejeani* should be ranked in a separate subgenus, and validate Puel's name since it has been accepted by other workers such as Csiki (1932).

The species *heros* and *dejeani* are closely related to those of the nominate subgenus as evidenced by the identical type of valvifer but warrant separate subgeneric status due to: bicolored rufotestaceous and bluish black dorsum; less prominently emarginate foretibial apex; broadly emarginate inner basal margin of the male foretibia; obtusely rounded apex of the female abdominal tergum VIII; and median lobe with shaft only very slightly arcuate and asymmetrical distally.

## 25 subgenus *Hexatrachus* Tschitscherine

(Figs. 192, 199, 222)

*Hexatrachus* Tschitscherine, 1898: 138. [TYPE SPECIES: *Harpalus poeciloides* Stephens, 1828, designated by Jeannel (1942)].

*Description.* — Body length 10 to 12 mm. Body form as in nominate subgenus.

Color. Various within species, dorsum of most specimens with metallic tinge.

Head. Labral apex slightly to moderately emarginate medially. Clypeus with 2 setae at each outer distal angle; apex straight to slightly emarginate medially. Frontal fovea with prominent clypeo-ocular prolongation. Mentum without or with slight tooth. Venter of head sparsely and irregularly pubescent. Paraglossa slightly longer than ligula.

Thorax. Pronotum pubescent near margins. Prosternum pubescent. Proepisternum pubescent anteriorly, glabrous posteriorly. Remainder of venter pubescent.

Legs. Forefemur of ♂ with obtuse tooth on apical 1/3 of posterior margin, tooth absent or weak in some specimens of *poeciloides*. Foretibia of ♂ (Fig. 192) with inner basal margin strongly and abruptly emarginate; unmodified in ♀; distal portion in both sexes moderately expanded laterally; apical spur trifid. Fore- and midtarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Hindfemur with numerous setae of various lengths along posterior margin. Hindtarsus relatively slender; segment I of most specimens equal to or longer than II + III. Dorsum of all tarsi sparsely pubescent.

Elytron. Rather flat in appearance, not prominently curved ventrad near apex; intervals VIII, IX, and X, or only IX and X pubescent basally and medially and in most specimens all intervals pubescent apically; interval III with 1 dorsal setigerous puncture near apical 1/3; interval III in most specimens and intervals V and VII in some specimens with series of apical setigerous punctures (larger than other punctures bearing pubescence).

Abdomen. Sternum I of some specimens, sterna II to IV of all specimens and proximal portion of sternum VI of some specimens pubescent (pubescence most prominent medially); sternum VI of ♂ with 2 pairs of ambulatory setae. Apex of ♀ tergum VIII (Fig. 199); more angulate than in nominate subgenus.

Male genitalia. Median lobe short and relatively stout; lacking apical disc; ventral and lateral surfaces with prominent longitudinal stria.

Female genitalia. Valvifer (Fig. 222) moderately sclerotized; flattened, similar in shape to that of nominate subgenus except broader and with blunter apex; distal portion with setae of various numbers and sizes; proximal lateral margin with membranous area.

*Discussion.* — This subgenus contains 3 species: *virens* Dejean, 1829, southwestern Europe and northern Africa; *poeciloides* (Stephens), 1828, England, central Europe to Norway and southern Russia, Balkan peninsula, and around northern border of Mediterranean to Persia;

and *mandschuricus* Jedlicka, 1942\* described from "Mandschuk" (possibly this refers to the Manchuria area of China). The former 2 species can be identified by keys in Puel (1931) and Jeannel (1942).

26 subgenus *Pseudodichirus* Lutshnik  
(Fig. 220)

*Pseudodichirus* Lutshnik, 1921: 3. [TYPE SPECIES: *Anisodactylus intermedius* Dejean, 1829, by monotypy].

*Description.* — Body length 12 to 14 mm. Body form as in nominate subgenus.

*Color.* Body piceous to black.

*Head.* Labral apex strongly emarginate medially. Clypeal apex slightly to moderately emarginate medially. Frons with fovea bearing clypeo-ocular prolongation and medially directed linear depression, producing a somewhat Y shaped fovea; microsculpture of isodiametric mesh. Mentum with tooth. Paraglossa slightly longer than ligula.

*Thorax.* Pronotum with sides strongly convergent basally. Prosternum pubescent except for median glabrous area.

*Legs.* Foretibial apical spur trifid. Hindtarsus relatively stout; segment I shorter than II + III. Dorsum of all tarsi with very sparse and irregular pubescence. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with segments II to IV laterally expanded and spongy pubescent beneath.

*Elytron.* Interval III with dorsal setigerous puncture adjoining stria II towards apical 1/3; intervals III, V, VII with 1 to several apical setigerous punctures.

*Hind wing.* Full and apparently functional.

*Abdomen.* Sternum VI of ♂ with 2 pairs of ambulatory setae. Apex of ♀ tergum VIII as in nominate subgenus.

*Male genitalia.* Median lobe lacking apical disc; membranous area of dorsum relatively long.

*Female genitalia.* Valvifer (Fig. 220) moderately sclerotized; subtriangular and with truncate apex; without setae; lateral margin somewhat membranous and indistinctly defined proximally.

*Discussion.* — This subgenus contains only the species *intermedius* which occurs all around the Mediterranean. Jeannel (1942) treated this subgenus as congeneric with the subgenus *Anisodactylus*. However *intermedius* warrants separate subgeneric status due to: female valvifer lacking setae and different in form (Fig. 220) from that constantly found in members of nominal subgenus (Figs. 217, 218); and mentum bearing moderate sized tooth (mentum of species in the nominate subgenus has at most a very small tooth in occasional specimens of some species). As discussed in the section on phylogeny, *intermedius* is the sister group of the subgenus *Gynandrotarsus*.

27 subgenus *Gynandrotarsus* LaFerté

*Gynandrotarsus* LaFerté, 1841a: 202. [TYPE SPECIES: *Gynandrotarsus harpaloides* LaFerté by monotypy].

*Triplectrus* LeConte, 1848: 381. [TYPE SPECIES: *Harpalus rusticus* Say, designated by Lindroth (1968)].

*Description.* — Body length 7.2 to 15.0 mm. Body rather stout and *Amara*-like.

*Color.* Body predominantly rufopiceous to black, except with slight greenish tinge to dorsum in many specimens of *opaculus* and with prominent greenish tinge to dorsum in all

specimens of *harpaloides*.

Head. Frontal fovea in some species bearing clypeo-ocular prolongation. Mentum unarmed or in most species with slight median tooth.

Thorax. Pronotum broad and wider than elytra measured across humeri in many species; side more or less rounded, not sinuate; lateral groove various; lateral bead, except in *haplo-mus*, evident along entire length from base to apex though in many species fine near apex; apical and basal beads distinct laterally, but obsolescent medially in most specimens. Prosternum glabrous medially, elsewhere with very fine short pubescence. Proepisternum glabrous except for short fine pubescence near anterior margin. Mesosternum of most specimens with fine short pubescence, glabrous in some specimens. Metasternum generally glabrous except for patch of fine short pubescence adjacent to midcoxa. Mesepisternum, mesepimeron, metepisternum, metepimeron glabrous.

Legs. Foretibia somewhat triangular due to strong lateral expansion of distal portion; anterior face with single row of 5 to 9 setigerous punctures extended proximally from apex; apex weakly emarginate with outer angle somewhat rounded and reduced (Fig. 45); apical spur strongly trifid (Fig. 45). Hindfemur with 2 long setae on posterior margin. Hindtarsus with segment I as long or longer than II + III. Last segment of all tarsi with 3 to 5 pairs of ventral setae. Fore- and midtarsi of ♂ with apex of segment I of most specimens and all of segments II to IV of all specimens laterally expanded and spongy pubescent beneath.

Elytron. Humerus with or without tooth; intervals flat to convex, glabrous in most specimens; intervals III (only V and VII in some *harpaloides*), V, and VII with apical series of setigerous punctures, arrangement and number of such punctures various within individual species.

Hind wing. Fully developed and apparently functional in all species.

Abdomen. Tergum VIII of ♂ with strongly angulate apex (Fig. 60).

Male genitalia. Median lobe symmetrical, except left side of apical disc slightly elevated in *ovularis*; surface with predominantly longitudinal striae which vary in arrangement and prominence within individual species, transverse stria also present in some specimens; with or without apical disc. Internal sac with small scales and scale-like spines, larger sclerotized structures present in *texanus*, *harpaloides*, *dulcicollis*, and *opaculus*; in repose appearing as simple tubular sac following shape of median lobe, except irregularly coiled inside median lobe in *dulcicollis*.

Female genitalia. Valvifer shaped as in Fig. 130, heavily sclerotized, glabrous, convex in ventral view except for concave distal area; convex distal portion in many specimens separated from proximal convex area by slight ridge, presence of ridge varied with individual species.

*Discussion.* — *Gynandrotarsus* was originally proposed as a separate genus by LaFerté (1841a). Subsequent authors treated it as a separate genus, as a subgenus, or as a species group of *Anisodactylus*. *Triplectrus* was proposed by LeConte (1848) as a subgenus of *Anisodactylus*, and most workers have so regarded it. Casey (1914) combined *Gynandrotarsus* and *Triplectrus*. Ball (1960a: 1963) accepted this union but pointed out that *Gynandrotarsus* has priority and treated the taxon as a subgenus of *Anisodactylus*.

Casey (1914) provided a key to the forms he recognized as valid and also proposed 5 new species. In 1924 Casey provided descriptions for 11 new species, but no key accompanied these descriptions. All of the species he proposed in 1924 and all but one of those proposed in 1914 are here regarded as conspecific with previously described species. Lindroth (1968) provided a fine revision of the northern species of *Gynandrotarsus*. However, he felt that there were additional southern forms and that a complete revision of the subgenus was warranted (personal communication). Such a revision has been done in this paper.

The union of *Triplectrus* and *Gynandrotarsus* and the treatment of this group as a subgenus of *Anisodactylus* seem well justified to me. The species *harpaloides* and *opaculus* ("true" *Gynandrotarsus*) are characterized by the foretarsus of the female having the first segment laterally expanded. However, as pointed out by Lindroth (1968) this expansion is also slightly developed in *dulicollis* and *texanus* ("true" *Triplectrus*), and these latter 2 species agree with the former 2 in having a clypeo-ocular prolongation on the frontal fovea of the head. The above 4 species and other species of the subgenus *Gynandrotarsus* share: trifold foretibial apical spur; short apical row of setigerous punctures on elytral intervals V and VII (also in most specimens on III); and type of female genitalia described above. Although well defined by the above combination of characters, *Gynandrotarsus* possesses no phenetically striking characters suggesting separate generic status on phenetic grounds, and there are no phylogenetic reasons for according it more than subgeneric status.

The species *carbonarius* was formerly treated as a member of the subgenus *Gynandrotarsus* because of its trifold foretibial apical spur. However, as explained in the discussion section on the subgenus *Anisodactylus*, this species belongs in the nominate subgenus.

### Key to the Species of the Subgenus *Gynandrotarsus*

*Notes concerning the key.*

Couplet 1 divides the species into 2 groups based primarily on presence or absence of a clypeo-ocular prolongation from the frontal fovea. All sections of each half of the couplet should be read before deciding in which group a given specimen belongs. The clypeo-ocular prolongation described in the first half of the couplet is varied in shape and direction as is the frontal fovea. In most specimens the fronto-clypeal suture as shown in Fig. 7 extends into the frontal fovea and then continues towards the eye as a linear depression or groove constituting the clypeo-ocular prolongation.

The presence or absence of a humeral tooth is used in couplets 8, 12, and 13; the humerus should be examined from directly above to determine if a tooth is present.

In couplet 8 males of *anthracinus* and *merula* are separated from males of *ovularis* and *darlingtoni* primarily by possessing a humeral tooth. I saw 3 males of *anthracinus* (all from Arizona), out of a total of approximately 200 males examined, which lacked a humeral tooth. Thus, approximately 1.5 percent of the male *anthracinus* keying to couplet 8 may be impossible to separate from *ovularis* and *darlingtoni* on the basis of only the humeral tooth character. Therefore, additional information has been provided on the median lobe of the species keying to couplet 8 to insure 100 percent correct determination of male *anthracinus*. The reader should also note that if the specimen is from southwestern Texas or Arizona, it probably is an *anthracinus* (whether a humeral tooth is present or not) since the other 3 species mentioned above are not recorded from these areas. I have not seen any Mexican specimens of *anthracinus* which lack a humeral tooth.

Some difficulty may be encountered in determining whether a humeral tooth is present on females of *merula* and *rusticus* which key to couplet 12. This is because occasional specimens of *rusticus* have a small primarily upward directed humeral denticle. When the humerus is examined in dorsal view, the denticle is not very evident in most specimens. I have seen 5 females with a vestigial laterally directed tooth and could not classify them to species since presence or absence of a humeral tooth is the sole known character of use in separating females of *rusticus* and *merula*.

The presence of a humeral tooth is used in couplet 13 to separate female *anthracinus* from female *ovularis* and *darlingtoni*. I have not yet encountered any females of *anthracinus* lacking a humeral tooth, but if the reader encounters a specimen which gives problems in this couplet, geographical distributions should be consulted. The range of *ovularis* is north

of those of *anthracinus* and *darlingtoni*, and of these 3 species only *anthracinus* is so far recorded from southwestern Texas and Arizona. The species *anthracinus* and *darlingtoni* are sympatric in Mexico. Many specimens of *darlingtoni* have a somewhat more slender body form than those of *anthracinus*. However, this slight difference in body form is not easy to note without large series of each species and is not as consistent or reliable for separating *anthracinus* and *darlingtoni* as presence or absence of a humeral tooth. No other characters are of practical use for separating females of these 2 species.

*Key to the Species of the Subgenus Gynandrotarsus*

- 1 Frontal fovea of head with clypeo-ocular prolongation toward eye (Fig. 46); OR clypeus lacking raised transverse ridge behind apex ..... 2
- Frontal fovea of head lacking clypeo-ocular prolongation; AND clypeus with raised transverse ridge behind apex ..... 5
- 2 (1) Dorsum dull black, not shiny, with prominent microsculpture; clypeus with raised transverse ridge behind apex; median lobe extremely narrow in lateral view, without apical disc (Figs. 111, 112); first segment of foretarsus of ♀ strongly expanded laterally (Fig. 43) ..... *opaculus* (LeConte), p. 358
- Dorsum shiny, microsculpture less developed; clypeus with or without raised transverse ridge behind apex; median lobe not as narrow (Figs. 118, 120, 124); first segment of foretarsus of ♀ various ..... 3
- 3 (2) Clypeus with raised transverse ridge behind apex; posterior pronotal angle not broadly rounded (Fig. 32); first segment of foretarsus of ♀ moderately expanded laterally (Fig. 42) ..... *texasus* (Schaeffer), p. 361
- Clypeus without raised transverse ridge behind apex; pronotal posterior angle various (Figs. 28, 31) ..... 4
- 4 (3) Dorsum with prominent greenish tinge, especially towards sides; abdominal sternum VI of ♂ with 2 pairs of ambulatory setae; median lobe without apical disc (Figs. 123, 124); first segment of foretarsus of ♀ very strongly expanded laterally, overlapping ventral base of segment II (Fig. 44) ..... *harpaloides* (LaFerté), p. 360
- Dorsum without prominent greenish tinge; abdominal sternum VI of ♂ with 1 pair of ambulatory setae; median lobe with prominent apical disc (Figs. 117, 118); first segment of foretarsus of ♀ only slightly expanded laterally (Fig. 41) ..... *dulcicollis* (LaFerté), p. 362
- 5 (1) Pronotal lateral bead fine basally and medially, obsolescent near anterior angle (Fig. 34); microsculpture of frons and pronotum consisting of very dense small isodiametric punctures; median lobe with apical disc (Figs. 113, 114) ..... *haplomus* Chaudoir, p. 363
- Pronotal lateral bead more prominent basally and medially, not obsolescent (though fine in some specimens) near anterior angle; microsculpture of frons consisting of isodiametric mesh, not of punctures; microsculpture of pronotum various, of isodiametric mesh in most specimens; median lobe with or without apical disc ..... 6
- 6 (5) Males, segments II to IV of fore- and midtarsus laterally expanded and spongy pubescent beneath ..... 7
- Females, segments II to IV of fore- and midtarsus neither laterally expanded or spongy pubescent beneath ..... 11
- 7 (6) Median lobe lacking apical disc (Figs. 115, 116) ..... (in part) *rusticus* (Say), p. 364
- Median lobe with apical disc (Figs. 109, 110, 121, 122, 125, 126) ..... 8

- 8 (7) Humerus in dorsal view with laterally projected tooth (Fig. 37); median lobe with left side of apical disc not elevated in dorsal view and membranous area of dorsum short (Figs. 121, 122) ..... 9
- Humerus in dorsal view lacking tooth (Fig. 36); median lobe with left side of apical disc elevated in dorsal view and membranous area of dorsum short (Figs. 125, 126) OR median lobe with left side of apical disc not elevated and membranous area of dorsum relatively long, extended in many specimens to basal bulb (Figs. 109, 110) ..... 10
- 9 (8) Body strongly convex, especially pronotum; pronotum not prominently widened basally and lateral depression not prominent (Fig. 30); range Davis Mts. of extreme western Texas, Arizona, New Mexico and Mexico (Fig. 160) ..... (in part) *anthracinus* (Dejean), p. 366
- Body not strongly convex; pronotum prominently widened basally and with prominent lateral depression rapidly widened basally (Fig. 29); range southeastern Canada, eastern United States (Fig. 161) ..... (in part) *merula* (Germar), p. 368
- 10 (8) Apical disc of median lobe shaped as in Fig. 125 and with left side slightly elevated in dorsal view; median lobe with membranous area of dorsum relatively short and shaft not strongly bent near basal bulb (Fig. 126); range southeastern Canada, eastern United States (Fig. 163) ..... (in part) *ovularis* (Casey), p. 372
- Apical disc of median lobe shaped as in Fig. 109 and with left side not elevated in dorsal view; median lobe with membranous area of dorsum relatively long, extended to basal bulb (Fig. 110) in many specimens; range northern and central Mexico (Fig. 157) ..... (in part) *darlingtoni* new species, p. 370
- 11 (6) Pronotum prominently widened basally (Figs. 27, 29) ..... 12
- Pronotum not prominently widened basally, side more evenly curved from apex to base (Figs. 26, 30, 35) ..... 13
- 12 (11) Humerus in dorsal view with prominent laterally directed tooth projected in most specimens well beyond outer edge of humerus (Fig. 37) ..... (in part) *merula* (Germar), p. 368
- Humerus in dorsal view without prominent laterally directed tooth (Fig. 36); in some specimens with slight mainly upward directed denticle (see discussion of characters used in this key) ..... (in part) *rusticus* (Say), p. 364
- 13 (11) Humerus in dorsal view with prominent laterally directed tooth projected in most specimens beyond lateral margin of humerus (Fig. 37) ..... (in part) *anthracinus* (Dejean), p. 366
- Humerus in dorsal view lacking tooth ..... 14
- 14 (13) Range southeastern Canada, eastern United States (Fig. 163); pronotum of many specimens with prominent lateral depression (Fig. 26) ..... (in part) *ovularis* (Casey), p. 372
- Range northern and central Mexico (Fig. 157); pronotum without prominent lateral depression (Fig. 35) ..... (in part) *darlingtoni* new species, p. 370

27.1 *Anisodactylus* (*Gynandrotarsus*) *opaculus* (LeConte)  
(Figs. 33, 43, 46, 111, 112, 158)

*Gynandrotarsus opaculus* LeConte, 1863: 16. [Holotype (MCZ), ♀ labeled: blood red disc without printing; "opaculus 2". TYPE LOCALITY: Texas as originally cited].

*Triplectrus paulus* Casey, 1924: 130. [Lectotype (USNM), here designated, ♂ labeled: "Tex", "Casey bequest 1925", "TYPE USNM 47942", "paulus Csy.". Additional label added stating: "LECTOTYPE *Triplectrus paulus* Casey By G. R. Noonan". TYPE LOCALITY: Austin, Texas as originally cited. NEW SYNONYMY].

*Description.* — Body length 8.6 to 12.2 mm.

Color. Dorsum black, dull due to prominent microsculpture, with faint greenish hue in some specimens; margins of labrum, clypeus and pronotum slightly lighter in some specimens. Venter, legs, and elytral epipleuron rufopiceous to black. Palpi and first 1 or 2 antennal segments rufotestaceous to piceous or castaneous; remaining antennal segments darker in most specimens.

Head. Labral apex straight to moderately emarginate medially. Clypeus with area immediately behind apex slightly elevated into low ridge and sloped proximally into shallow, fine groove; apex straight to moderately emarginate medially. Frons with fovea punctiform, bearing clypeo-ocular prolongation; microsculpture of prominent isodiametric mesh. Mental tooth absent to prominent.

Thorax. Pronotum as in Fig. 33; lateral depression obsolescent to moderate; lateral bead moderately prominent; basal fovea shallow, linear to elliptical; microsculpture of prominent isodiametric mesh.

Legs. Dorsum of tarsi glabrous to sparsely pubescent. Foretarsus of ♀ with segment I strongly expanded laterally (Fig. 43) but not as greatly as in *harpaloides*.

Elytron. Humerus (posterior aspect) of most specimens with rudimentary tooth; intervals flat to slightly convex; stria moderately prominent in most specimens; subapical sinuation obsolescent or absent; microsculpture of prominent slightly granulate isodiametric mesh.

Abdomen. Sternum VI of ♂ with 2 pairs of ambulatory setae.

Male genitalia. Median lobe (Figs. 111, 112) very narrow in lateral aspect; without apical disc; membranous area of dorsum short in most specimens. Everted internal sac with distal portion bearing varied series of scale-like spines similar to those in *dulcicollis*.

*Variation.* — Intrapopulational variation occurs in: color; body size and to a slight degree body proportions; emargination of labral and clypeal apices; presence or absence of mental tooth; prominence of pronotal lateral depression; humeral tooth; convexity of elytral intervals; prominence of elytral stria and subapical sinuation; and number and arrangement of scale-like spines on internal sac.

*Discussion.* — The LeConte collection at MCZ contains a series of 8 *opaculus*. The first specimen is a male labeled: blood red disc without printing, "7", "Type 5948", "C. opaculus Salle Lec.". This specimen cannot be the holotype since LeConte said his single specimen was a female given to him by a Mr. Ulke and stated "the terminal spur of the anterior tibiae is broken. . .". The male specimen labeled as a type evidently came from Salle and has both terminal spurs intact. The second specimen is a female labeled: blood red disc without printing, "opaculus 2". This specimen has both terminal spurs broken (only specimen in the series with the spurs so damaged), fits LeConte's description, and is the true holotype.

The form *paulus* was distinguished from *opaculus* by Casey (1924) on the basis of smaller body size, shorter prothorax, deeper and coarser elytral stria, more convex elytral intervals, and smaller head. These characters vary within *opaculus*, and the lectotype of *paulus* bears no characters warranting separate status from *opaculus*.

*Flight.* — Members of this species have been taken frequently at lights throughout its range and apparently are ready fliers.

*Bionomics.* — Members of this species have been collected from January to August and in November but appear to be most common in June, July and August.

Ball's data indicate *opaculus* has been taken: in dry leaf litter on damp soil in woods of

hackberry trees with varied rather open undergrowth on the Blackstone Ranch, 16 mi. S. of Sheffield, Texas; and Ball has collected specimens as they crawled at dusk over bare dry ground in an area of scrub desert with mesquite on the Blackstone Ranch, 13 mi. S. of Sheffield, Texas. Label data on specimens indicate that: 1 female was found in the soil of a peach orchard in Caddo County, Louisiana; 2 females were taken along a pond margin 5 mi. N. of Dilley, Texas; 2 males, 2 females were collected in pit fall traps in a region of tall grass in Davis County Arkansas; 1 male was taken under stones at Gainesville, Texas; and 1 female from under dried cow chips at Victoria, Texas.

Forbes (1883) reported that the gut contents of 2 specimens of *opaculus* consisted of seeds and other vegetable matter.

*Distribution and material examined* (699 specimens). The species *opaculus* is found in the south central United States, and 1 specimen has been taken in Mexico, 5 mi. W. Iturbide, Nuevo Leon (Fig. 158). I have also seen 2 specimens labeled as being from Long Island, New York, but believe they are mislabeled since this is far north of the established range.

## 27.2 *Anisodactylus (Gynandrotarsus) harpaloides* (LaFerté)

(Figs. 31, 44, 123, 124, 159)

*Gynandrotarsus harpaloides* LaFerté, 1841a: 203. [Lectotype (MNHP), here designated, ♀ labeled: "harpaloides m. Po. in texas.", "Ex Musaeo Chaudoir". Additional label added stating: "LECTOTYPE *Gynandrotarsus harpaloides* LaFerte By G. R. Noonan". TYPE LOCALITY: Texas as originally cited].

*Triplectrus beryllus* Casey, 1924: 131. [Lectotype (USNM), here designated, ♂ labeled: "McPher Ks", "Casey bequest 1925", "TYPE USNM 47973", "beryllus Csy.". Additional label added stating: "LECTOTYPE *Triplectrus beryllus* Casey By G. R. Noonan". NEW SYNONYMY].

*Description.* — Body length 8.2 to 10.9 mm.

Color. Dorsum piceous to black, margins of labrum, clypeus, and pronotum lighter in some specimens; center of frons with rufescent spot in some specimens; head and pronotum of some specimens with greenish tinge, such tinge more prominent along pronotal sides and in area of pronotal basal fovea; elytron of most specimens with prominent greenish tinge. Venter and coxae rufopiceous to black. Trochanters, femora, tibiae, palpi and first 1 or 2 antennal segments testaceous to rufopiceous or castaneous; tarsi and remainder of antenna darker in most specimens.

Head. Labral and clypeal apices straight to slightly emarginate medially. Frons with fovea punctiform, bearing clypeo-ocular prolongation; microsculpture of isodiametric mesh, obsolescent medially in most specimens. Mentum without tooth.

Thorax. Pronotum (Fig. 31) with anterior angle somewhat less prominent than in *dulcicollis*; posterior angle moderately rounded; lateral depression obsolescent in most specimens; lateral bead prominent; basal fovea shallow, linear to slightly elliptical, in most specimens with scattered punctures; microsculpture of isodiametric mesh, obsolescent medially in most specimens.

Legs. Foretarsus of ♀ with segment I very strongly expanded laterally, plate-like, and overlapping ventral base of segment II (Fig. 44).

Elytron. Humerus without tooth; intervals flat to slightly convex; subapical sinuation obsolescent; microsculpture of isodiametric mesh.

Abdomen. Sternum VI of ♂ with 2 pairs of ambulatory setae.

Male genitalia. Median lobe (Figs. 123, 124) relatively slender; without apical disc; membranous area of dorsum short to long, in some specimens extended nearly to basal bulb;



ventral and lateral sides with longitudinal striae in most specimens. Everted sac bearing proximal very discrete field of scale-like spines and apical less sharply defined field of scale-like spines.

*Variation.* — Intrapopulational variation exists in: body size; color; and emargination of labral and clypeal apices.

*Discussion.* — I have examined the male lectotype, 2 male paralectotypes and the female paralectotype of *beryllus*. All four specimens have a conspicuous greenish tinge to the dorsum and lack a raised ridge behind the clypeal apex. The males have the form of median lobe found only in *harpaloides* while the female has the first segment of the foretarsus very strongly expanded laterally. There is no reason to regard *beryllus* as a separate species.

*Bionomics.* — Members of this species have been collected in January and from March to September. As discussed under the species *dulcicollis*, I collected *harpaloides* in association with *dulcicollis* and *ovularis* in a pasture 2.7 mi. W. of Millington, Tennessee on September 16, 1969. All of the *harpaloides* were slightly teneral. Label data on the material examined indicate that *harpaloides* has been taken as follows: 1 female in sedge grass, Arkansas County, Arkansas; 1 male associated with cotton, Jefferson County, Arkansas; and 1 male and 1 female under a stone, Atchison County, Kansas.

*Distribution and material examined* (62 specimens). This species is known from Arkansas, Florida, Kansas, Louisiana, Oklahoma, Missouri, Tennessee, and Texas (Fig. 159).

### 27.3 *Anisodactylus (Gynandrotarsus) texanus* Schaeffer

(Figs. 32, 42, 119, 120, 164)

*Anisodactylus (Triplectrus) texanus* Schaeffer, 1910: 404. [Lectotype (USNM), here designated, ♂ labeled: "N. Braunfels, Tex.". Additional label added stating: "LECTOTYPE *Anisodactylus texanus* Schaeffer By G. R. Noonan". TYPE LOCALITY: New Braunfels, Texas as originally cited].

*Description.* — Body length 9.5 to 12.2 mm.

*Color.* Dorsum shiny dark piceous to black; margins of labrum, clypeus, and pronotum lighter in some specimens. Venter and legs piceous to black. Palpi rufous to black or infuscated. Antenna with segment I testaceous to rufopiceous; remaining segments somewhat darker.

*Head.* Labral apex straight to slightly emarginate medially. Clypeus with apex straight to slightly emarginate medially; raised transverse ridge present behind apex. Frons with fovea punctiform, bearing clypeo-ocular prolongation; microsculpture of isodiametric mesh, obsolete medially. Mentum without tooth.

*Thorax.* Pronotum (Fig. 32) with posterior angle slightly obtuse, not broadly rounded as in *dulcicollis*; lateral depression obsolescent; lateral bead prominent, especially near posterior angle; basal fovea shallow, linear to slightly elliptical, with scattered punctures in most specimens; microsculpture obsolescent medially, elsewhere of isodiametric mesh.

*Legs.* Dorsum of tarsi glabrous in most specimens. Foretarsus of ♀ with segment I moderately expanded laterally (Fig. 42).

*Elytron.* Humerus (in posterior aspect) of most specimens with rudimentary tooth; intervals flat to moderately convex; subapical sinuation obsolescent; microsculpture isodiametric, nearly obsolescent in ♂, normal in ♀.

*Abdomen.* Sternum VI of ♂ with 2 pairs of ambulatory setae.

*Male genitalia.* Median lobe (Figs. 119, 120) with prominent apical disc; dorsum of apex between distal end of membranous area and apical disc concave and laterally bounded by raised ridge formed from sides of median lobe. Everted internal sac bearing varied armature,

consisting in most specimens of proximal field of moderate sized scale-like spines and more distally situated fields of small scale-like spines.

*Discussion.* — The collection at USNM contains several specimens with written labels stating "N. Braunfels, Tex." The handwriting on the labels may well be that of Schaeffer (Kenneth Cooper, personal communication). Lindroth (1968) reported he could not locate types of *texanus* at the USNM. I feel these specimens are part of the original type series and have (above) designated one as the lectotype.

*Flight.* — One female was taken by light at Boquillas in Big Bend National Park, Texas.

*Bionomics.* — Members of this species have been collected from February to August. Ball's data indicate specimens have been taken: under stones on damp ground with sparse vegetation near small water impoundment in desert region on the Cochran Ranch, Sanderson, Texas; under cover of bent, coarse grass, tree branches, and stones along roadside ditch and depression filled with water by recent rains in normally arid region 16 mi. N. of Dryden, Texas; in dry leaves on damp clay soil in a stand of evergreen oaks near Independence Creek in the vicinity of the Pecos River, Texas; in dry leaf litter on damp soil in woods of hackberry trees with varied rather open undergrowth 16 mi. S. Sheffield; as beetles crawled over surface of bare dry ground at dusk in scrub desert with mesquite 13 mi. S. Sheffield, Texas; and under stones in gravel pit on slight slope in desert region with acacia shrubs and few grasses at Villa Lopez, Mexico.

*Distribution and material examined* (109 specimens). This species is found in southern Arizona, Louisiana, Texas, and northern Mexico (Fig. 164).

#### 27.4 *Anisodactylus (Gynandrotarsus) dulcicollis* (LaFerté)

(Figs. 28, 41, 45, 117, 118, 165)

*Harpalus dulcicollis* LaFerté, 1841b: 44. [Lectotype (MNHP), designated by Lindroth (1968 and 1969a), ♂ labeled: "Ex Musaeo Chaudoir", "TYPE". TYPE LOCALITY: Texas as originally cited].

*Anisodactylus (Tripectrus) ellipticus* LeConte, 1848: 384. [Type (MCZ), ♂ labeled: orange disc without printing, "Type 5967", "A. ellipticus Lec", "dulcicollis 6". TYPE LOCALITY: New Orleans, Louisiana as originally cited].

*Anisodactylus (Gynandrotarsus) elongatus* Chaudoir, 1868: 163. [Holotype (MNHP), ♂ labeled: "Ex Musaeo Chaudoir", "Texas Salle.", "TYPE", "dulcicollis Laf. det Lindroth 67". TYPE LOCALITY: Texas as originally cited].

*Tripectrus modicus* Casey, 1914: 178. [Lectotype (USNM), designated by Lindroth (1968 and 1969a), ♀. TYPE LOCALITY: Houston, Texas as originally cited].

*Description.* — Body length 8.5 to 11.8 mm.

Color. Dorsum somewhat shiny, especially on pronotum, black or very dark piceous; in some specimens margins of labrum, clypeus, and pronotum lighter; pronotal sides translucent in some specimens; elytron with faint aeneous tinge in some specimens. Venter, legs, and elytral epipleuron rufopiceous to black. Palpi and first 2 antennal segments testaceous to rufotestaceous or castaneous; remaining antennal segments same or slightly darker.

Head. Labral and clypeal apices straight to slightly emarginate medially. Mentum without tooth or small tooth present. Frons with fovea punctiform, in most specimens bearing clypeo-ocular prolongation; microsculpture of isodiametric mesh, obsolete medially in many specimens.

Thorax. Pronotum (Fig. 28) with prominent anterior angle; posterior angle broadly rounded; lateral depression obsolescent; lateral bead moderately prominent; basal fovea shallow, linear to elliptical, with scattered punctures in most specimens; microsculpture obsolescent

medially, elsewhere of isodiametric mesh.

Legs. Dorsum of tarsi glabrous to sparsely pubescent. Foretarsus of ♀ with segment I slightly expanded laterally (Fig. 41).

Elytron. Humerus (posterior aspect) of some specimens with faint rudimentary tooth; intervals flat to slightly convex; subapical sinuation obsolescent; microsculpture of isodiametric mesh, slightly granulate in ♀.

Abdomen. Sternum VI of ♂ with 1 pair of ambulatory setae.

Male genitalia. Median lobe (Figs. 117, 118) in dorsal view with sides somewhat parallel just before apex; with prominent apical disc; ventral surface with prominent longitudinal striae in many specimens. Internal sac relatively long and in repose irregularly coiled within median lobe; everted sac showing several large scale-like spines near distal end and bearing various very small spines and scales.

*Variation.* — Intrapopulational variation occurs in: body size; color; emargination of labral and clypeal apices; mental tooth; pronotal basal fovea; humeral tooth; convexity of elytral intervals; striae of median lobe; and number and arrangement of large scale-like spines and small spines and scales on internal sac.

*Discussion.* — The forms *ellipticus*, *elongatus* and *modicus* were correctly treated as conspecific with *dulcicollis* by Lindroth (1968).

*Flight.* — Specimens of *dulcicollis* have been collected at lights throughout its range and are evidently ready fliers.

*Bionomics.* — Members of this species have been taken from throughout the year but appear to be most common during April to August.

On October 16, 1969, I collected 14 males and 11 females of *dulcicollis* in a pasture 2.7 mi. W. Millington, Tennessee. The species was associated with *harpaloides* and *ovularis* and together with them was restricted to the tops and sides of small hills where the ground was well drained, exposed to sun during the entire day, and covered with only a sparse growth of short grass. All of the specimens of these 3 species were found during the day resting on the surface of the ground (or in short tunnels just below the surface) beneath dried cow chips. I also collected in well drained areas receiving shade from trees but found no *Gynandrotarsus* in such areas. Other areas of the pasture which received sun all day but were less well drained and had a denser grass cover also contained no *Gynandrotarsus*.

Label data indicate specimens have been taken: from pit fall traps in regions of tall grass at several localities in Louisiana; from cultivated lands such as strawberry fields, cottonfields, peach orchards, rice levies, gardens and sweet potato fields; under bark of rotting logs; under *Opuntia*; in pastures; under stones; and associated with trash.

*Distribution and material examined* (420 specimens). This species is found in the southern and central part of the eastern United States (Fig. 165). I have also seen 1 specimen labeled as from the Huachuca Mts. of Arizona, 1 labeled as from Los Angeles County, California, and 1 labeled as from Colorado.

### 27.5 *Anisodactylus (Gynandrotarsus) haplomus* Chaudoir (Figs. 34, 113, 114, 166)

*Anisodactylus (Gynandrotarsus) haplomus* Chaudoir, 1868: 163. [Holotype (MNHP), ♀ labeled: "bor", "Ex Musaeo Chaudoir", "Type". TYPE LOCALITY: Not originally cited, Galveston, Texas designated by Lindroth (1968)].

*Triplectrus peropacus* Casey, 1914: 175. [Lectotype (USNM), designated by Lindroth (1968 and 1969a), ♂. TYPE LOCALITY: Galveston, Texas to District of Columbia originally cited, restricted to Galveston, Texas by Lindroth (1968)].

*Triplectrus breviceps* Casey, 1924: 129. [Holotype (USNM), ♀. TYPE LOCALITY: Mobile, Alabama as originally cited].

*Triplectrus longicollis* Casey, 1924: 129. [Holotype (USNM), ♂ labeled: "D.C.", "Casey bequest 1925", "TYPE USNM 47973", "longicollis Csy.". TYPE LOCALITY: District of Columbia as originally cited. NEW SYNONYMY].

*Description.* — Body length 9.9 to 15.0 mm.

Color. Dorsum black, margins of labrum lighter in some specimens. Venter and legs rufopiceous to black. Palpi rufopiceous to black or infuscated. Antenna with first 1 or 2 segments testaceous to rufopiceous; remaining segments darker in most specimens.

Head. Labral apex straight to moderately emarginate medially. Clypeus with apex straight to slightly emarginate medially; with transverse raised ridge immediately behind apex. Frons with fovea punctiform; microsculpture of small dense isodiametric punctures. Mentum of most specimens without tooth.

Thorax. Pronotum (Fig. 34) widened basally; anterior margin somewhat less emarginate and anterior angle more rounded than in *rusticus*; lateral depression relatively wide, especially basally, not sharply delimited, evident to anterior angle; lateral bead fine, becoming obsolescent just behind anterior angle; basal fovea shallow, irregular or linear, in most specimens with few scattered punctures; microsculpture as on frons.

Elytron. Humerus without tooth; intervals slightly to strongly convex; subapical sinuation prominent and deep; microsculpture of isodiametric punctures, under certain lighting conditions appearing as granulate mesh.

Abdomen. Sternum VI of ♂ with 1 or 2 pairs of ambulatory setae.

Male genitalia. Median lobe (Figs. 113, 114) with apical disc; dorsum between distal end of membranous area and apical disc slightly convex; apex bent ventrad; membranous area of dorsum short, not reaching basal bulb.

*Variation.* — Intrapopulational variation exists in: body size; color; emargination of labral and clypeal apices; presence or absence of mental tooth; convexity of elytral intervals.

*Discussion.* — The forms *peropacus* and *breviceps* were correctly treated by Lindroth (1968) as conspecific with *haplomus*; their types have: pronotal lateral bead obsolescent near anterior angle; pronotal microsculpture of isodiametric punctures; humerus without tooth; and elytral subapical sinuation prominent. The form *longicollis* was said by Casey to differ from *peropacus* by being narrower and smaller and having the anterior male tarsi less strongly dilated; but these characters vary somewhat within *haplomus*, and the type of *longicollis* possesses the characters of *haplomus*.

*Flight.* — Members of this species have been taken at light in May and June at a number of localities and are apparently ready fliers.

*Bionomics.* — Members of this species have been collected in March to August, November, and December but appear to be most common in May and June.

*Distribution and material examined* (193 specimens). This species is known from scattered localities in eastern United States (Fig. 166).

## 27.6 *Anisodactylus (Gynandrotarsus) rusticus* (Say)

(Figs. 27, 40, 115, 116, 162)

*Harpalus rusticus* Say, 1823: 32. [Neotype (MCZ), designated by Lindroth (1969b), ♂ labeled: "Rumney, N. H. VI-30 1924 Baker R.", "♂", "P. J. Darlington Collection", "Neotype Harpalus rusticus Say design. Lth.", "Anisodactylus rusticus Say det. Lindroth 68.". TYPE LOCALITY: Not originally cited, restricted to Rumney, New Hampshire by Lindroth (1968)].

*Anisodactylus tristis* Dejean, 1829: 158. [Lectotype (MNHP), here designated, ♂ labeled: "♂", "tristis. m. in Amer. bor.", "Beauvois", "Anisod. rusticus Say. box 207.". Additional label added stating: "LECTOTYPE *Anisodactylus tristis* Dejean By G. R. Noonan". TYPE LOCALITY: "Amer. sept." originally cited].

*Triplectrus oblongus* Casey, 1924: 128. [Holotype (USNM), ♀. TYPE LOCALITY: Nisbet, Pennsylvania as originally cited].

*Description.* — Body length 7.2 to 12.6 mm.

Color. Dorsum rufopiceous to black; margins of labrum, clypeus, and pronotal base lighter in some specimens; in most specimens sides of pronotum rufescent or translucent, especially posteriorly. Venter rufopiceous to black. Legs rufopiceous to black, in most specimens femora darker than other segments. Palpi testaceous to black or infuscated, apices lighter in most specimens. Antenna with first 2 segments testaceous or rufous in most specimens, infuscated in a few specimens; remaining segments darker in most specimens.

Head. Labral apex slightly to moderately emarginate medially. Clypeus with apex moderately to strongly emarginate medially, base of labrum exposed in some specimens; transverse ridge present behind apex. Frons with fovea punctiform; microsculpture of prominent isodiametric mesh. Mentum of most specimens without tooth.

Thorax. Pronotum (Fig. 27) prominently widened basally; lateral depression prominent, strongly widened basally; lateral bead moderate, in most specimens narrowed just before posterior angle; basal fovea various, linear or elliptical in many specimens; microsculpture medially of isodiametric mesh, elsewhere appearing as isodiametric punctures or slightly granulate mesh depending on lighting.

Elytron. Humerus (in dorsal view) without tooth except for few specimens possessing vestigial tooth (see discussion under variation); intervals flat to strongly convex; subapical sinuation obsolescent; microsculpture of isodiametric punctures with tendency to be arranged in irregular chains.

Abdomen. Sternum VI of ♂ with 1 pair of ambulatory setae.

Male genitalia. Median lobe (Figs. 115, 116) without apical disc; tip bent ventrad in many specimens.

*Variation.* — Intrapopulational variation exists in: body size; color; microsculpture; emargination of labral and clypeal apices; pronotal basal fovea; and convexity of elytral intervals. I have seen 4 males with vestigial humeral teeth, but they clearly are *rusticus*; their median lobes lack apical discs. The 4 specimens are from: Mt. Toby Massachusetts; E. Hartford, Connecticut; Rockaway Beach, Long Island, New York; and Clemson, South Carolina. In addition, I have seen 5 females with vestigial humeral teeth; they may be either *merula* or aberrant *rusticus*. These females are from: Berryville, Arkansas; Prospect Park, Long Island, New York; Dallas, Texas; Mt. Mitchel, North Carolina; and Washington County, Arkansas.

*Discussion.* — The form *tristis* has correctly been regarded as conspecific with *rusticus* since shortly after its description. Further, the form *oblongus* was correctly treated as conspecific with *rusticus* by Lindroth (1968). Possible problems in separating aberrant specimens of *rusticus* from specimens of *merula* are treated in the introduction to the species key.

*Flight.* — Lindroth (1968) reported *rusticus* as being "Found in great numbers in wind-drift material on the north-shore of L. Erie. . . certainly a good flier." One female was taken in March as it flew in a pasture south of Creedmoor, Granville County, North Carolina. One female and 1 male were taken in April and August respectively at lights at Nevada, Vernon County, Missouri. Three females were taken at electric lights in April, May, and June at Washington, D.C.

*Bionomics.* — Members of this species have been taken throughout the entire year but

appear to be most common in May to August. Lindroth (1968) reported *rusticus* is found "On dry, sandy fields with thin but often tall vegetation. During daytime hiding under the plants."

In May I took 9 males and 9 females in an old gravel pit at Forestville, Maryland, 6.2 mi. W. of Washington, D. C. The specimens were found on moist gravel soil beneath debris in areas receiving sun throughout the entire day. The ground had a very scattered and sparse grass cover. In July T. and L. Erwin and I (as described under the species *ovularis*) collected 5 males of *rusticus* along with a female *ovularis* on the edge of a grassy field 4.1 mi. W. of Paris, Clarke County, Virginia.

Label data on material examined indicates *rusticus* has been taken: in sand dunes west of Johnson, Vermont; in a gravel pit at Middlebury, Vermont; on soil under dead grass in a peach orchard in Stoddard County, Missouri; from a 5 year old *Pinus sylvestri* plantation in Wexford County, Michigan; under debris on the shore of Lake Michigan, Michigan; in grassland at Manhattan, Kansas; in broom sedge in White County, Arkansas; in cotton in Pope County, Arkansas; in areas of Karmax and Amiban grass in Washington County, Arkansas; under corn stalks near Ethylsville, Alabama; and washed up at Rockaway Beach, Long Island, New York.

Johnson and Cameron (1969) reported that a specimen of *rusticus* fed on grass seed in the laboratory.

*Distribution and material examined* (1,150 specimens). This species is centered in eastern United States and southeastern Texas (Fig. 162). It ranges from Prince Edward Island (Lindroth, 1968) in the northeast to Yellowstone National Park, Wyoming (2 males) and Greeley, Weld County, Colorado (1 female) in the northwest, southward to Arizona (Casey, 1924) and south to Cuero, De Witt County, Texas (1 female).

### 27.7 *Anisodactylus* (*Gynandrotarsus*) *anthracinus* (Dejean) (Figs. 30, 37, 160)

*Harpalus anthracinus* Dejean, 1829: 369. [Holotype (MNHP), ♀ labeled: "♀", "Harpal", "anthracinus. m in Mexico", "Höpfner", "Ex Musaeo Chaudoir", "Bates vidit 1881". TYPE LOCALITY: Mexico as originally cited].

*Anisodactylus dilatatus* Say, 1834: 431. [Neotype (MCZ), here designated, ♂ labeled: "37 mi. west of Durango, DGO. 8400'. 3 18 1963 W.S. Creighton". Additional label added stating: "Neotype *Anisodactylus dilatatus* design. G. R. Noonan". TYPE LOCALITY: Mexico cited by Say, here restricted to 37 mi. W. Durango, Durango, Mexico].

*Triplectrus convexus* Casey, 1914: 176. [Lectotype (USNM), here designated, ♂ labeled: "Ari.", "Casey bequest 1925", "TYPE USNM 47938", "convexus Csy.". Additional label added stating: "LECTOTYPE *Triplectrus convexus* Casey By G. R. Noonan". TYPE LOCALITY: Arizona originally cited, here restricted to Madera Canyon, Pima County, Arizona. NEW SYNONYMY].

*Description.* — Body length 11.3 to 14.9 mm.

Color. Dorsum dark piceous to black except margins of labrum, clypeus, and pronotum may be lighter. Venter and legs rufopiceous to black. Palpi testaceous to piceous. Antenna with first segment testaceous to piceous; remaining segments darker in most specimens.

Head. Labral apex slightly to moderately emarginate medially. Clypeus with apex slightly to moderately emarginate medially, base of labrum exposed in many specimens; with low transverse ridge behind apex. Frons with fovea punctiform, in some specimens bearing medially directed impression; microsculpture of isodiametric mesh, may be obsolescent medially, especially in ♂; surface may be wrinkled. Mentum without or with slight tooth.

Thorax. Pronotum (Fig. 30) very convex (much more so than in *merula*; not prominently widened basally; lateral bead moderate; surface wrinkled in some specimens; basal fovea various, in many specimens linear or elliptical; microsculpture of isodiametric mesh. obsolete medially in many specimens, especially in ♂.

Elytron. Humerus (in dorsal view) with tooth (Fig. 37) (except for 3 ♂♂ as mentioned in section on variation); intervals flat to moderately convex; subapical sinuation obsolescent; microsculpture of isodiametric mesh in ♂, in ♀ appearing either as isodiametric punctures or granulate isodiametric mesh depending on lighting conditions.

Abdomen. Sternum VI of ♂ with 1 pair of ambulatory setae.

Male genitalia. As in *merula*.

*Variation.* — Intrapopulational variation occurs in: body size; color; microsculpture; emargination of labral and clypeal apices; frontal fovea; pronotal basal fovea; degree of convexity of elytral intervals. One female from 6 mi. E. of Queretaro, Queretaro, Mexico is unique in bearing 2 long setae at the right distal outer angle of the clypeus. The humeral tooth is vestigial and difficult to discern in: a male from 18 mi. S.W. of Bowie, near Apache Pass, Cochise County, Arizona; a male from the eastern slope of the Galiuro Mountains, Graham County, Arizona; and a male from Madera Canyon, Santa Rita Mountains, Arizona. However, all other characters in these 3 males are those "normal" for the species *anthracinus*.

*Discussion.* — I above designate a neotype for *dilatatus*. The entire insect collection of Say was destroyed except for a few specimens sent to Dejean in France (Lindroth and Freitag, 1969b). The Oberthür collection at the MNHP contains 4 males and 2 females by the name label "*dilatatus* Say Mexique". However, none of these specimens bear the green labels characteristic of specimens in the Dejean collection or any other indication that they came from the Dejean collection. All but one specimen, a female, belong to the species *anthracinus*. The female belongs to *darlingtoni*, a new species named in this paper. The original description of *dilatatus* provides no worthwhile clues as to which species or even which subgenus of *Anisodactylus* the original *dilatatus* referred to. However, past authors have treated *dilatatus* as conspecific with *anthracinus*, and in the interest of taxonomic stability I select as neotype a specimen which is a member of this species. The neotype is deposited at MCZ.

Casey (1914) separated *convexus* from *anthracinus* primarily by the arrangement of setigerous punctures along the third elytral interval, but this character varies within *anthracinus* and other species of *Gynandrotarsus*. The lectotype and paralectotypes of *convexus* are all clearly members of the species *anthracinus*.

Males of *anthracinus* and *merula*, clearly allopatric forms (Fig. 160, 161), have the same genitalia. To decide relationships I noted their external differences, and compared these external differences with those found in other pairs of closely related species of *Gynandrotarsus*. Specimens of *anthracinus* differ from *merula* by: more convex body; pronotum not prominently widened basally, much more convex than in *merula*, and with narrow or obsolescent lateral depression. Many specimens of the species pairs *merula* and *haplomus* and *rusticus* and *merula* differ no more from one another externally than do *anthracinus* from *merula*. As to the identical genitalia of *merula* and *anthracinus*, there is no *a priori* reason why genitalia must always be different in separate species. The external features separating *anthracinus* and *merula* are constant and are sufficient to warrant retaining *anthracinus* as a valid species.

*Flight.* — One female was taken at light in August at Peña Blanca, Arizona, and 1 male and 2 females were taken at light in June at the Southwest Research Station, 5 mi. W. Portal, Arizona.

*Bionomics.* — Members of this species have been taken in January and from March to

November but appear to be most common in June, July, and August. In September of 1964 and 1969, I collected 23 *anthracinus* on or adjacent to Procter's Ranch at the entrance to Madera Canyon, Pima County, Arizona. The area was primarily desert-like with ocotillo, barrel cactus, mesquite, yuccas, and various grasses. During the day specimens were found resting under dried cow chips and rocks. After approximately 17:40 (Pacific Standard Time) they were found mainly crawling over the surface of the ground. All the sites containing *anthracinus* received sun during most of the day. In September, I also took 3 specimens in the collecting area at the Southwest Research Station described under the species *Notiobia brevicollis*.

Ball's data indicate specimens have been taken: under cover on sandy clay soil with grasses in a pinon pine, juniper, and evergreen oak forest in the Davis Mountains, Texas; under cover of stones, leaves, bark, and fallen logs in area with walnut, willow, and poplar trees in Limpia Canyon, Davis Mountains, Texas; under cover on damp, bare clay soil on eastern slope of the Galiuro Mountains, Graham County, Arizona; under dried cow chips on sandy clay soil in grassy meadow with many flowers and some shrubs 18 mi. S.W. Bowie near Apache Pass, Cochise County, Arizona; under rocks on sandy soil in desert scrub area 6 mi. E. Queretaro, Mexico; under stones on reddish clay soil in vicinity of small pond with vegetation of grasses and herbs in semi-desert country 33 km. N. of Acambay, Mexico; under cover on east facing slope with cut-over tropical deciduous forest and grassy meadows below the trees 9.5 mi. W. of Morelia, Mexico; and under *Acacia* shrubs on dam face, in litter, and under cover in unshaded places in area of acacia-grassland mainly in vicinity of small reservoir on west side of road 13 mi. S.E. of Lagos de Moreno, Mexico.

*Distribution and material examined* (427 specimens). This species is found: in the Davis Mountains of extreme southwestern New Mexico; highland or mountainous areas of Arizona (few specimens seen labeled as from Tucson and Phoenix but probably collected in nearby mountains or else taken at light); Tulare County, California (based on single specimen in Van Dyke Collection at California Academy of Sciences); and in the central and northern highlands of Mexico (Fig. 160). The Mexican part of its range is sympatric with that of *darlingtoni*, and the two species occur together at a number of localities in Mexico.

### 27.8 *Anisodactylus (Gynandrotarsus) merula* (Germar)

(Figs. 29, 121, 122, 161)

*Harpalus merula* Germar, 1824: 24. [Lectotype (MNHP), designated by Lindroth (1968 and 1969a), ♀ labeled: "Merula Germar in Amer. bor. D.", "to", "Germar", "Ex Musaeo Chaudoir", "Lectotype merula Germ. design. Lindroth". TYPE LOCALITY: Kentucky as originally cited].

*Anisodactylus (Triplectrus) crassus* LeConte, 1848: 382. [Lectotype (MCZ), designated by Lindroth (1968 and 1969a), ♀ labeled: pink disc without any printing, "269", "Type 5951", "crassus Lec.", "rusticus 16". TYPE LOCALITY: New York (whether city or state not certain) as originally cited].

*Anisodactylus (Triplectrus) gravidus* LeConte, 1848: 383. [Lectotype (MCZ), designated by Lindroth (1968 and 1969a), ♀ labeled: pink disc without any printing, "Type 5949", "gravidus Lec.", "rusticus". TYPE LOCALITY: New York (whether city or state not certain) as originally cited].

*Anisodactylus (Triplectrus) pinguis* LeConte, 1848: 382. [Lectotype (MCZ), designated by Lindroth (1968 and 1969a), ♀ labeled: green disc without any printing, "267", "Type 5950", "A. pinguis Lec.", "rusticus 14". TYPE LOCALITY: "ad Rocky Mountains" as originally cited].



*Triplectrus aethiops* Casey, 1914: 175. [Lectotype (USNM), here designated, ♀ labeled: "Tex", "Casey bequest 1925", "TYPE USNM 47932", "aethiops Csy". Additional label added stating: "LECTOTYPE Triplectrus aethiops Casey By G. R. Noonan". TYPE LOCALITY: Austin and Waco, Texas originally cited, restricted to Austin by Casey in 1924. NEW SYNONYMY].

*Triplectrus kemp*i Casey, 1924: 130. [Holotype (USNM), ♀. TYPE LOCALITY: Lake George, New York as originally cited].

*Triplectrus marginatus* Casey, 1924: 126. [Holotype (USNM), ♂ labeled: "Mich", Casey bequest 1925", "TYPE USNM 47934", "marginatus Csy". TYPE LOCALITY: Grayling, near Bay City, Michigan as originally cited].

*Triplectrus sulcipennis* Casey, 1924: 128. [Lectotype (USNM), here designated, ♀ labeled: "Tex Waco", "TYPE USNM 47931", "sulcipennis Csy". Additional label added stating: "LECTOTYPE Triplectrus sulcipennis Casey By G. R. Noonan". TYPE LOCALITY: Waco, Texas as originally cited. NEW SYNONYMY].

*Triplectrus wolcott*i Casey, 1924: 127. [Lectotype (USNM), designated by Lindroth (1968 and 1969a), ♀. TYPE LOCALITY: Northern Illinois near Chicago as originally cited].

*Description.* — Body length 9.9 to 14.1 mm. Body less convex than in *anthracinus*. Color. Dorsum rufopiceous to black; margins of labrum, clypeus, and pronotum lighter in some specimens. Venter and legs rufopiceous to black. Palpi testaceous to piceous. Antenna with first 2 segments testaceous to rufopiceous; remaining segments darker in most specimens.

Head. Labral apex slightly to moderately emarginate medially. Clypeus with apex moderately to strongly emarginate medially, base of labrum exposed in some specimens; transverse ridge present behind apex. Frons with fovea punctiform; microsculpture of isodiametric mesh, may be less prominent medially.

Thorax. Pronotum (Fig. 29) not strongly convex; prominently widened basally; lateral depression prominent and rapidly widened basally in most specimens; lateral bead moderate; basal fovea various, in many specimens linear or elliptical; microsculpture in ♂ appearing as isodiametric slightly granulate mesh or as isodiametric punctures depending on lighting, in ♀ appearing as isodiametric granulate mesh or as isodiametric punctures depending on lighting, less prominent medially in many specimens of both sexes but still evident.

Elytron. Humerus (in dorsal view) with tooth (Fig. 37); intervals flat to strongly convex; subapical sinuation obsolescent; microsculpture appearing as granulate isodiametric mesh or isodiametric punctures depending on lighting.

Abdomen. Sternum VI of ♂ with 1 pair of ambulatory setae.

Male genitalia. Median lobe (Figs. 121, 122) rather stout; with prominent apical disc; membranous area of dorsum relatively short and rapidly narrowing proximally, not reaching region of basal bulb.

*Variation.* — Intrapopulational variation exists in: body size; color; microsculpture; emargination of labral and clypeal apices; pronotal basal fovea; and convexity of elytral intervals.

*Discussion.* — Lindroth (1968) correctly treated *crassus*, *gravidus*, *pinguis*, *kemp*i, *wolcott*i, and *marginatus* as conspecific with *merula*; their types all clearly fall within the boundary of the description given above for *merula*. It is difficult to discern what separating characters Casey (1914) envisioned for *aethiops* other than "form less stout". The type series of *aethiops* was originally composed of 3 specimens. In 1924 Casey split this series and declared the 2 specimens from Austin, Texas to be members of a new species, *sulcipennis*, stated to be broader in form than *aethiops* and to have more convex elytral intervals.

The lectotypes of *aethiops* and *sulcipennis* are neither narrower nor broader than many specimens of *merula* and are clearly members of this species.

Larger examples of *merula* with black body color and microsculpture appearing of isodiametric punctures may resemble *haplomus*. But they are distinguished by the moderately prominent pronotal lateral bead which in *haplomus* is fine basally and obsolescent near the anterior angle.

*Flight*. — Only 3 specimens are labeled as taken at light: 1 female at an incandescent light in April at Fort Clinch State Park, Florida; 1 female in a light trap at Tyler, Texas; and 1 female at a light at Glen Burnie, Maryland. I have examined 1,134 specimens of *merula* and, therefore, it appears members of this species do not fly readily.

*Bionomics*. — Members of *merula* have been collected throughout the entire year but seem most common in June, July and August. Lindroth (1968) stated that specimens of *merula* are found "On very dry, sandy ground with scattered vegetation." Label data reveal that specimens have been taken as follows: under rocks and dried cow chips in a number of localities; 1 male, 1 female from *Geomys* burrows 20 mi. S. of San Antonio, Texas; 21 specimens from a *Pinus sylvestris* plantation in Wexford County, Michigan; from soil of peach orchards in Louisiana, Missouri, and North Carolina; in grasslands of Riley County, Kansas; 1 female on cotton in Florida; 1 female on corn at Winnsboro, Louisiana; 1 female under strawberries at Amite, Louisiana; 1 male under stone on dry sandy hill at Billerica, Massachusetts; 1 male under log on dry hillside at Rumney, New Hampshire. One male and 3 females glued on a single card are labeled as having been observed eating eggs of *Pantamorus peregrinus* laid on a small twig.

*Distribution and material examined* (1,134 specimens). The species *merula* is found along the southeastern boundary of Canada, and in the eastern United States (Fig. 161). The dot in southern California is based on a female labeled as from Anaheim, California (in collection of The Academy of Natural Sciences of Philadelphia). I have seen 3 specimens recorded as from Kentucky, a few from along the margin of Lake Michigan in Illinois and Indiana, and one labeled as from Pennsylvania. Aside from these specimens it seems that *merula* is either absent or very scarce in most of Illinois, Indiana, Ohio, Kentucky, Virginia, West Virginia, Pennsylvania, and eastern New York.

### 27.9 *Anisodactylus* (*Gynandrotarsus*) *darlingtoni* NEW SPECIES

(Figs. 35, 36, 109, 110, 157)

Holotype. Male. Mexico, Michoacan Rte. 15, e. Morelia 7000', creek and arid pasture VIII.5.62, H. E. Evans Exp., George E. Ball Collector.

*Description*. — Body length 10.9 mm.

Color. Dorsum with head black except margins of labrum and clypeus slightly lighter; pronotum black; elytron dark piceous. Venter and legs piceous to black. Palpi rufous to piceous. Antenna with first segment castaneous; remaining ones darker.

Head. Labral apex slightly emarginate medially. Clypeus with apex slightly emarginate medially; raised transverse ridge present behind apex. Frons with fovea punctiform; microsculpture of isodiametric mesh.

Thorax. Pronotum (Fig. 35) with side evenly rounded from apex to base, not widened basally; lateral depression obsolescent; lateral bead moderate; apical bead complete but flattened medially; basal fovea very shallow, linear; microsculpture of isodiametric mesh.

Elytron. Humerus (Fig. 36) (in dorsal view) without tooth; intervals slightly convex; subapical situation obsolescent; microsculpture of isodiametric mesh.

Abdomen. Sternum VI bearing 1 pair of ambulatory setae.

Genitalia. Median lobe (Figs. 109, 110) with apical disc; tip of apex bent ventrad; membranous area of dorsum long, extended nearly to basal bulb, relatively wide and occupy-

ing most of dorsal width until near its proximal end.

*Allotype*. — Female. Same label data as holotype. Body length 12.5 mm. Distal 3 segments of left antenna missing. Microsculpture of dorsum of granulate isodiametric mesh; on elytron each granule with visible depression in center. Sternum VI of abdomen with 2 pairs of ambulatory setae. Genitalia as described for females in subgenus description. Remainder as in holotype.

*Paratypes and Variation*. — Body length 9.1 to 12.5 mm. The dorsum of some specimens has the pronotal side rufescent, and the second antennal segment of some specimens is light colored as the first. The dorsum is slightly wrinkled in some specimens. The labral and clypeal apices vary from straight to moderately emarginate within populations. The microsculpture of the male and female paratypes is as described respectively for the holotype and allotype. The membranous area of the dorsum of the median lobe is slightly shorter than in the holotype in some males; however, it is always relatively longer and wider than in *merula*. The following paratypes were examined (133 specimens): MEXICO: DISTRITO FEDERAL: San Angel, 5 ♂♂, 2 ♀♀. DURANGO: 25 mi. W. Durango, 1 ♀, VI-29-1964. JALISCO: 13.0 mi. S.E. Lagos de Moreno, Rte. 45, 6,540 feet, reservoir, 1 ♀, IX-7-1967. MEXICO: El Yukon, Rte. 15, W. Toluca, 8,800 feet, 2 ♂♂, 1 ♀, VIII-8-1962; Toluca, 7 ♂♂, 11 ♀♀, 34 km. W. Toluca, Rte. 15, 8,500 feet, 4 ♂♂, creek margin, VIII-9-1962. MICHOACAN: Huajumbaro, Rte. 15, 8,500 feet, 1 ♂, pasture, VIII-5-1962; 4.0 mi. N.W. Jiquilpan, Rte. 110, 5,950 feet, 1 ♀, VIII-2-1967; 13.0 mi. S.E. Lagos de Moreno, Rte. 45, 6,450 feet, 1 ♀, reservoir IX-7-1967; Lago Patzcuaro, 3 ♂♂, 4 ♀♀, VIII-29-1945; E. Morelia, Rte. 15, 7,000 feet, 5 ♂♂, 2 ♀♀, creek and arid pasture, VIII-5-1962; 9.5 mi. W. Morelia, Rte. 15, 6,250 feet, 18 ♂♂, 8 ♀♀, tropical-deciduous forest, VIII-18-1967; 6 km. E. Quiroga, Rte. 15, 7,000 feet, 11 ♂♂, 10 ♀♀, roadside pasture, VIII-6-1962; near Tzintzuntzan, 7,000 feet, 1 ♂, 3 ♀♀, roadside, VIII-6-1962; 50 mi. W. Zitacuaro, 19 ♂♂, 4 ♀♀, IX-19-1938. QUERETARO: 33 km. N. Acambay, Rte. 55, 7,600 feet, 2 ♂♂, 1 ♀, pond and semi-desert, VIII-8-1962. SONORA: Yecora, 7,000 feet, 2 ♂♂, 2 ♀♀, V-20-22-1961. No locality other than country given, 1 ♀.

*Deposition of type material*. — The holotype and allotype are deposited at MCZ while the paratypes are deposited at CAS, Canadian National Collection at Ottawa, Canada, MCZ, UASM, and USNM.

*Derivation of name*. — It gives me great pleasure to name this species after P.J. Darlington, Jr., who very kindly offered me encouragement and assistance on numerous occasions.

*Flight*. — No data available.

*Bionomics*. — Members of *darlingtoni* have been collected in May, June, August, and September and are most common in August. Label data indicate specimens have been taken at altitudes from 5,950 to 8,500 feet. Ball's data indicate specimens have been collected as follows: the holotype, allotype, and 5 paratypes under stones on north facing slope several feet from small probably intermittent stream in semi-desert grassland east of Morelia; under cover in a cut-over tropical deciduous forest on east facing slope above grassy meadow 9.5 mi. W. of Morelia; under stones on reddish clay soil in vicinity of small pond with vegetation of grasses and herbs in semi-desert country 33 km. N. of Acambay; under stones on damp red clay soil in roadside pasture 6 km. E. of Quiroga; under cover in grassy grazed field with some *Acacia* bushes and black clay soil 4 mi. N.W. Jiquilpan; under *Acacia* bushes on dam face, in litter, and under cover in unshaded places in area of acacia-grassland mainly in vicinity of small reservoir on west side of road 13 mi. S.E. of Lagos de Moreno.

*Distribution*. — This species is found in the highlands of central and northern Mexico (Fig. 157).

27.10 *Anisodactylus (Gynandrotarsus) ovularis* (Casey)  
(Figs. 26, 125, 126, 163)

*Triplectrus ovularis* Casey, 1914: 177. [Lectotype (USNM), designated by Lindroth (1968 and 1969a), ♂. TYPE LOCALITY: St. Louis, Missouri and Salina, Kansas cited by Casey, restricted to St. Louis, Missouri by Lindroth (1968)].

*Triplectrus semirubidus* Casey, 1924: 127. [Holotype (USNM), ♀. TYPE LOCALITY: Highland Park, north of Chicago, Illinois as originally cited].

*Description.* — Body length 9.0 to 13.6 mm.

Color. Dorsum dark piceous to black; margins of labrum and sides of pronotum lighter in some specimens. Venter and legs rufous to black. Palpi and first 2 antennal segments testaceous to rufopiceous or infuscated; remaining segments of antenna darker in most specimens.

Head. Labral apex straight to moderately emarginate medially. Clypeus with apex straight to moderately emarginate medially; area immediately behind apex slightly elevated into low transverse ridge sloped proximally into shallow fine groove. Frons with fovea punctiform; microsculpture of isodiametric mesh. Mentum of most specimens without tooth.

Thorax. Pronotum (Fig. 26) much less widened basally than in *rusticus*, *haplomus*, and most *merula*; side evenly rounded; lateral depression moderate; lateral bead prominent; basal fovea shallow, linear to slightly elliptical in form, with few scattered punctures in most specimens; microsculpture of isodiametric mesh.

Elytron. Humerus without tooth; intervals flat to slightly convex; subapical situation obsolescent; microsculpture of dense, mostly triangular punctures, may appear as slightly granulate mesh under certain lighting conditions.

Abdomen. Sternum VI of ♂ with 1 pair of ambulatory setae.

Male genitalia. Median lobe (Figs. 125, 126) relatively elongate and slender; with apical disc; left side of disc in dorsal view slightly more elevated than right side; membranous area of dorsum short; ventral surface in most specimens with prominent longitudinal striae and dorsal surface and sides with obsolescent longitudinal striae.

*Discussion.* — The holotype of *semirubidus* possesses the pronotal form characteristic for *ovularis*, lacks a humeral tooth, and as determined by Lindroth (1968) is clearly conspecific with *ovularis*.

*Flight.* — One female was taken at light in June at Glen Burnie, Maryland, and 1 male and 1 female were collected at light in May at Chouteau, Oklahoma.

*Bionomics.* — Members of this species have been taken in January and from April to December but most have been taken in May, June, and July. Lindroth (1968) reported that in Canada *ovularis* has been "Found only on the N shore of L. Erie, mainly in drift material, probably as a straggler from the south."

As discussed under the species *dulcicollis*, I have collected *ovularis* in association with *dulcicollis* and *harpaloides* in a pasture 2.7 mi. W. of Millington, Tennessee. During the afternoon of July 3, 1971, T. and L. Erwin and I collected 1 female *ovularis* by digging up herbs and grasses on the edge of a grassy field 4.1 mi. W. of Paris, Virginia. The collecting site was located on a slight slope with well leached soil, scattered grass, and weeds and was exposed to sun from approximately mid-morning to late afternoon. Several specimens of *rusticus* were also taken in this site by digging up plants near the edge of the grassy field. The grassy field had a dense cover of grasses and weeds of approximately 1 to 2 feet height, and no *Gynandrotarsus* were found in it.

Label data indicate specimens have been taken as follows: 1 female on ground; 3 males, 1 female under boards in pasture; and 1 female from nest of *Microtus ochrogaster* at Urbana,

Illinois; 2 males, 2 females from commercial orchard at Kearneysville, West Virginia; 1 female in ocean drift at Ocean Beach, Fire Island, New York; and 1 female under log near the Patuxent River, Maryland.

*Distribution and material examined* (277 specimens). This species is primarily centered in the plains area of east central United States but is known from as far south as Texas and Mississippi, as far north as southern Canada, and as far east as New Jersey and New York (Fig. 163).

28 subgenus *Anadaptus* Casey  
(Figs. 176, 188, 189, 190, 206, 207)

*Anadaptus* Casey, 1914: 203. [TYPE SPECIES: *Anisodactylus discoideus* Dejean, 1831, designated by Lindroth (1968)].

*Description*. — Body length 8.3 to 13.2 mm. Body convex and subcylindrical, somewhat stouter in *discoideus*.

Color. Various.

Head. Labral apex slightly to strongly emarginate medially. Clypeus with apex straight to slightly emarginate medially; 1 to 4 setigerous punctures at each outer distal angle depending on species. Frons with frontal fovea (if not obscured by punctures) somewhat linear and with clypeo-ocular prolongation; with or without median single or double rufous spot; microsculpture of most specimens obsolete medially and elsewhere of isodiametric mesh. Mentum without tooth or in some specimens with vestigial tooth.

Thorax. Pronotum somewhat cordiform, sinuate behind in most species; posterior angle acute to slightly obtuse, broadly rounded in *rotundangulus*; lateral depression various; lateral bead complete; apical and basal beads present laterally and in most specimens also medially; microsculpture of most specimens obsolete medially and elsewhere of isodiametric mesh. Prosternum completely pubescent in *viridescens*, with glabrous median area in other species. Proepisternum glabrous except for occasional fine short setae at anterior end. Mesosternum pubescent. Mesepisternum and mesepimeron pubescent, except in some examples of *discoideus*. Metasternum and metepisternum of most specimens with some pubescence.

Legs. Foretibia with distal portion laterally expanded; apical spur of most specimens angulate near base but extremely varied, grading (Figs. 188, 189, 190) within individual species from relatively slender (Fig. 188) to (few specimens) subtrifid (Fig. 190). Hind tarsus stout and short; segment I shorter than II + III. Dorsum of all tarsi sparsely pubescent except in some *discoideus*; last segment with 3 to 6 pairs of ventral setae. Fore- and mid-tarsus of ♂ with apex of segment I in some specimens and all of segments II to IV in all specimens laterally expanded and spongy pubescent beneath.

Elytron. Humerus with small tooth in some specimens; intervals flat to convex; pubescence and punctuation restricted to sides and apex or expanded over entire elytron, concentrated on even intervals when so expanded; microsculpture of isodiametric mesh, but more prominent and subgranulate in some ♀♀, and nearly obsolete in ♂♂ of *discoideus*.

Abdomen. Sterna with pubescence varied according to species; sternum VI of ♂ with 1 or 2 pairs of ambulatory setae. Apex of tergum VIII of ♀ rounded.

Male genitalia. Median lobe (Figs. 206, 207) with "button"-like apical disc; membranous area long, extended nearly to basal bulb in most specimens. Internal sac without armature.

Female genitalia. Valvifer moderately sclerotized and slightly convex in ventral view; distal portion with setae of various numbers and sizes; shape greatly varied, changing from lobed to non-lobed within several species as presently defined.

*Discussion*. — Casey (1914) proposed *Anadaptus* as a separate genus apparently on the

basis of the narrow, convex body form and cordiform pronotum of its species. However, body form in *discoideus* is certainly as stout as that in other subgenera of *Anisodactylus*, and cordiform pronota occur in other subgenera. Lindroth (1968) correctly treated *Anadaptus* as a subgenus of *Anisodactylus*.

Casey (1914) produced a key to the species which he recognized as *Anadaptus*, but like most of his keys, it was difficult to use and excessively split species. Lindroth (1968) revised the Canadian species and some of the United States ones and provided a key to all the Canadian and many of the United States forms; he has suggested (personal communication) that the more southern forms need additional work.

The species *rotundangulus* was originally described as an *Anisodactylus* by Bates (1878a) and also treated as a member of this genus in his classic work (1882) on the Carabidae of Central America. Csiki (1932) listed the species as a member of *Anisotarsus*, probably as an unintentional error since he did not follow his usual practice of citing in parentheses the original genus in which the species was proposed. Van Emden (1953) did not mention the species in his revision of *Anisotarsus*. The species *rotundangulus* is a member of the genus *Anisodactylus* and of the subgenus *Anadaptus*, and shares the following characters with other members of *Anadaptus*: mentum and submentum completely fused (as in all species of the genus *Anisodactylus* but in no members of *Anisotarsus*); hindtarsus short and with segment I shorter than II + III; dorsum of all tarsi sparsely pubescent; apex of female abdominal tergum VIII rounded; median lobe with prominent "button"-like apical disc; internal sac without armature; and valvifer moderately sclerotized, with setae distally and lobed as in several other species within the subgenus.

The species *rotundangulus* is presently known only from central Mexico. The other 7 species are found in Canada and the United States and are: *alternans* LeConte, 1849; *discoideus* Dejean, 1831; *nivalis* Horn, 1880; *porosus* Motschulsky, 1845; *pitychrous* LeConte, 1861; *sanctaecrucis* (Fabricius), 1798; and *viridescens* LeConte, 1861.

#### 29 subgenus *Spongopus* LeConte (Figs. 179, 185, 230)

*Spongopus* LeConte, 1848: 377. [TYPE SPECIES: *Spongopus verticalis* LeConte, 1848, by monotypy].

*Description.* — Body length 12.8 to 14.0 mm. Body with short, cordate prothorax and long, parallel sided elytra.

*Color.* Body black or dark piceous on dorsum; frons with large rufous spot; venter and appendages lighter than dorsum.

*Head.* Mandible prolonged with pointed, arcuate apex; dorsal surface striate. Labral apex strongly emarginate medially. Clypeal apex straight in most specimens. Frons with fovea small, elliptical, deep pit continued posteriorly toward eye as shallow clypeo-ocular prolongation; microsculpture of isodiametric mesh, obsolete medially in most specimens. Mentum with or without tooth. Paraglossa (Fig. 179) of most specimens slightly longer than ligula and with apices bent towards ligula.

*Thorax.* Pronotum (Fig. 185) short, broad, cordate (often more so than in Fig. 185); side straight or slightly sinuate before obtuse but prominent posterior angle; disc with scattered, generally fine punctures. Prosternum pubescent. Proepisternum, mesosternum, mesepisternum, mesepimeron, metasternum, and metepisternum pubescent.

*Legs.* Foretibia with distal portion slightly expanded laterally; apical spur stout, slightly swollen at base in some specimens. Hindfemur with 2 long setae and several shorter ones on posterior margin. Hindtarsus with segment I slightly shorter than II + III. Last segment of

all tarsi with 4 to 5 pairs of ventral setae. Fore- and midtarsi of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Intervals finely, irregularly covered with non-setigerous punctures; outer 2 or 3 intervals pubescent; interval III in most specimens with dorsal setigerous puncture adjacent to stria II about 1/3 distance from apex.

Abdomen. Sterna with irregular pubescence, such pubescence denser and more regular anteriorly on abdomen; sternum VI of ♂ with 1 pair of ambulatory setae. Tergum VIII of ♀ with rounded apex.

Male genitalia. Median lobe stout, slightly swollen medially; lacking apical disc; membranous area of dorsum various, proximal boundaries may be difficult to distinguish, in some specimens with an elongate narrow extension reaching area of basal bulb; field of scale-like spines (arising from internal sac) may project from ostium. Everted internal sac with irregular mushroom like shape and with gonopore situated on side; with 2 fields of armature, basal one (which in most specimens projects through ostium when sac in repose) consisting of scale like spines, apical field of elongate spines.

Female genitalia. Valvifer (Fig. 230) moderately sclerotized, slightly convex; lateral margin membranous and irregular in some specimens; with 1 seta on distal mesal margin in most specimens. Stylus of most specimens with basal segment bearing 1 or 2 very small setae on distal lateral margin.

*Discussion.* — This subgenus contains only the species *verticalis* LeConte, 1848 found in southeastern Canada and eastern United States.

*Spongopus* has been treated by most workers, although often with reservations, as an independent genus. However, Lindroth (1968) showed that it is best regarded as a subgenus of *Anisodactylus*. He pointed out that the single character of any value that might justify keeping *Spongopus* as a separate genus is the mental tooth described by many authors, but further noted that this tooth actually varies from absent to well developed (though always more obtuse and less prominent than in *Anisotarsus*). I have confirmed this observation and also noted that in other species of *Anisodactylus* the mental tooth varies in the same manner. The general habitus of *Spongopus* is certainly distinctive but does not warrant generic separation. And as noted by Lindroth the elongate, pointed, striate mandibles and the elongate labrum, which have also been used to justify separate generic status, may be adaptations to a predatory mode of living.

### 30 subgenus *Aplocentrus* LeConte (Figs. 203, 223)

*Aplocentrus* LeConte, 1848: 385. [(*Haplocentrus* auct.) TYPE SPECIES: *Harpalus caenus* Say, 1823, designated by Lindroth (1968)].

*Description.* — Body length 7.8 to 11.5 mm. Body broad and *Amara*-like.

Color. Body piceous to black. Dorsum with metallic greenish, aeneous, bronze, or bluish tinges.

Head. Labral apex moderately to strongly emarginate medially. Clypeal apex straight to slightly emarginate medially. Frontal fovea bearing prominent clypeo-ocular prolongation. Mentum without tooth in most specimens. Paraglossa slightly longer than ligula.

Thorax. Pronotum relatively broad; lateral depression prominent; microsculpture of isodiametric mesh. Prosternum densely pubescent in *amaroides*, more sparsely so and often with median glabrous area in *caenus*. Proepisternum of many specimens pubescent anteriorly, glabrous posteriorly. Remainder of venter pubescent in most *amaroides* and glabrous or nearly glabrous in *caenus*.

Legs. Foretibia with distal portion moderately expanded laterally; apex emarginate, outer angle of emargination prominent in most *amaroides* and more rounded in most *caenus*; apical spur prominently swollen or somewhat angulate near base in *amaroides*, not or only slightly swollen near base in *caenus*. Hindfemur with various numbers of long setae on posterior margin. Dorsum of all tarsi glabrous or pubescent; last segment with 4 to 5 pairs of ventral setae. Hindtarsus with first segment longer in most *caenus* and shorter in most *amaroides* than II + III. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with apex of segment I in some specimens and all of segments II to IV in all specimens laterally expanded and spongy pubescent beneath.

Elytron. Intervals generally flat; interval III with 1 dorsal puncture near apical 1/3.

Abdomen. Sternum VI of ♂ with 2 pairs of ambulatory setae. Tergum VIII of ♀ with triangular apex (Fig. 203).

Male genitalia. Median lobe with apex in dorsal view slightly deflected to right in *caenus*.

Female genitalia. Valvifer (Fig. 223) lightly sclerotized, thin and platelike, somewhat triangular; distal margin with 1 to 4 setae. Stylus with basal segment bearing 2 or 3 setae on distal lateral margin.

*Discussion.* — *Aplocentrus* has been given different status and regarded as including different species by various authors. In his fine work on North American *Anisodactylus* Lindroth (1968) correctly regarded *Aplocentrus* as a subgenus of that genus. However, Lindroth placed *caenus* and *laetus* in *Aplocentrus* while placing *amaroides* in a separate informal group of apparently equal weight to a subgenus. The species *laetus* warrants separate subgeneric status, and I place it in the new subgenus *Pseudaplocentrus* for reasons discussed under that taxon.

Lindroth placed *amaroides* in a separate group from *caenus* because he felt the former species had: hind tarsus with segment I shorter than II + III and hardly exceeding elongate apical spur of hindtibia; foretibial apex more strongly emarginate and with outer angle of emargination not rounded; and apical spur of foretibia basally swollen. In contrast, *caenus* was reported to have: hind tarsus with segment I as long as II + III and much longer than apical tibial spur; foretibia with outer angle of emargination more rounded; and apical spur of foretibia slender. In samples of 15 specimens of each species, the ratio of the length of the first segment of the hindtarsus divided by the combined lengths of II + III varies from 0.75 to 0.91 in *amaroides* and from 0.86 to 1.3 in *caenus*; while the ratio of the length of the first segment of the hindtarsus divided by the length of the hindtibial apical spur varies from 0.856 to 1.07 in *amaroides* and from 1.0 to 1.4 in *caenus*. The strength of the emargination and prominence of the outer angle of the foretibial apex vary considerably within each of the species and are not stable enough for reliable separation. The apical spur of the foretibia does seem to be swollen or even slightly angulate near the base in all *amaroides*, but the spur in *caenus* varies somewhat more and in some specimens is slightly swollen near the base.

The species *amaroides* and *caenus* are in fact closely related by their similar valvifers, similar apex on female eighth abdominal tergum, and presence of setae on basal segment of stylus. The subgenus *Aplocentrus*, as defined here, then includes 2 species: *amaroides* LeConte, 1851 from western Canada and western United States; and *caenus* (Say), 1823 from eastern Canada and eastern United States. These species are closely related on morphological grounds, exhibit spatial vicariance, and in my opinion are sister species.



31 subgenus *Pseudaplocentrus* NEW SUBGENUS  
(Figs. 202, 225)

TYPE SPECIES: *Anisodactylus laetus* Dejean, 1829, by present designation and monotypy.

*Description.* — Body length 8.0 to 9.0 mm. Body relatively narrow.

Color. Body piceous to black. Dorsum with metallic green or aeneous tinge. Appendages of most specimens lighter than body.

Head. Frontal fovea bearing clypeo-ocular prolongation. Eye very large and strongly protruding. Mentum without tooth in most specimens. Paraglossa membranous, slightly longer than ligula.

Thorax. Pronotum with wide flattened lateral depression abruptly set off from disc by prominent inflexion of integument except inflexion absent in basal 1/5 though flattened lateral depression still apparent there; flattened lateral depression translucent in many specimens; lateral, apical and basal beads present.

Legs. Hindfemur with 2 to 4 long setae on posterior margin. Hind tarsus with segment I shorter than II + III. Fore- and midtarsi of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Intervals convex; striae extremely prominent, simirectangular in cross section; interval III with 1 dorsal setigerous puncture approximately 1/2 distance from apex.

Abdomen. Sternum VI of ♂ with 2 pairs of ambulatory setae. Tergum VIII of ♀ with rounded apex (Fig. 202).

Male genitalia. Median lobe with ventral surface somewhat serrate in lateral view.

Female genitalia. Valvifer (Fig. 225) thick, heavily sclerotized, slightly convex in ventral view; without setae; distal portion with prominent ridge from which surface sharply slopes towards apex and sides. Stylus with basal segment bearing 2 or 3 setae on distal lateral margin.

*Discussion.* — This subgenus contains only the species *laetus* Dejean, 1829 found in the eastern United States. Various authors have included this species in *Aplocentrus* or simply placed it in *Anisodactylus* without subgeneric assignment. Actually, *laetus* warrants separate subgeneric status because the following apomorphic features are absent in other species of *Anisodactylus*: eye large and protruding; pronotum with lateral depression as described above; and elytral striae extremely prominent and semirectangular in cross section.

32 genus *Geopinus* LeConte  
(Figs. 195, 196, 200, 226, 236)

*Geopinus* LeConte, 1848: 271. [TYPE SPECIES: *Daptus incrassatus* Dejean, 1829, by monotypy].

*Description.* — Body length 13 to 17.0 mm. Body rather stout, head with broad neck, and prothorax small and narrow.

Color. Pale rufotestaceous, pronotum of most specimens with darker median area, and elytron with at least inner striae darker and inner intervals somewhat infuscated.

Head. Mandible stout, strongly arcuate; apex deeply striate. Labral apex moderately emarginate medially. Gena in front of eye with broad sulcus receiving first antennal segment when in repose. Eye small. Frons with fovea small, elliptical; microsculpture obsolescent. Mentum without tooth. Mentum and submentum completely fused. Ligula strongly expanded laterally at apex. Paraglossa slightly shorter than ligula.

Thorax. Pronotum narrow, only slightly wider than head; lateral bead complete but fine; apical and basal beads present; microsculpture obsolescent.

Legs. Foretibia (Fig. 195) with apical portion strongly expanded laterally; with large excavate dilation at external apex; apical spur slender or slightly swollen medially. Distal portion of mid- and hindtibia strongly expanded laterally. Hindfemur of most specimens with more than 10 long setae on posterior margin. Hindtibia with spatulate apical spur. Hindtarsus short, strongly tapering distally (Fig. 196); segment I shorter than II + III. All tarsi with segment I to IV bearing numerous prominent lateral and latero-ventral spines; segment V with 2 to 5 pairs of ventral setae; dorsum of all segments glabrous. Foretarsus of ♂ with segments II to IV moderately expanded laterally and sparsely spongy pubescent beneath. Midtarsus of ♂ unmodified.

Elytron. Scutellar stria lacking ocellate puncture at base; humerus rounded; without dorsal punctures; microsculpture of weak fine isodiametric mesh along side, base, and apex, obsolescent elsewhere.

Abdomen. Sterna with varied short pubescence (absent on sternum VI in most specimens) and varied numbers of long ambulatory setae. Tergum VIII of ♀ with very broadly rounded apex (Fig. 200).

Male genitalia. Median lobe with ostium in median position; lacking apical disc. Internal sac without armature.

Female genitalia. Valvifer (Fig. 226) moderately sclerotized, slightly convex and with numerous distal setae. Stylus (Fig. 236) with basal segment bearing several prominent setae on distal lateral margin; apical segment elongate, with long setae arising close together on distal 1/3 and with several irregularly distributed shorter setae.

*Discussion.* — This genus contains only the species *incrassatus* (Dejean), 1829 found in the eastern half of the United States and southern Canada. For a long time *Geopinus* was placed in the subtribe Daptini. However, Ball (1960a) pointed out that the males of *Geopinus* do have spongy pubescence on the venter of the foretarsus and a symmetric median lobe and concluded that *Geopinus* could be placed in the subtribe Anisodactylina. Lindroth (1968) agreed and suggested that the antennal sulcus on the head and the modified fore- and midtibia of *Geopinus* are adaptations to its fossorial mode of living. I agree completely with the conclusions of Ball and Lindroth.

### 33-34 genus *Amphasia* Newman

*Amphasia* Newman, 1838: 388. [TYPE SPECIES: *Amphasia fulvicollis* Newman, 1838, by monotypy, = *interstitialis* Say, 1823].

*Description.* — Body length 8.5 to 14.0 mm. Body relatively slender, covered with dense pubescence.

Head. Mentum without tooth. Mentum and submentum completely fused.

Thorax. Pronotum with side evenly rounded; posterior angle broadly rounded; lateral bead complete; apical and basal beads present at least laterally. Prosternum pubescent. Proepisternum of most specimens pubescent anteriorly and glabrous posteriorly. Mesosternum, mesepisternum, mesepimeron, metasternum, metepisternum, and metepimeron pubescent.

Legs. Foretibia with distal portion slightly expanded laterally. Hindtarsus slender; segment I slightly shorter to slightly longer than II + III. Dorsum of all tarsi pubescent; last segment with 4 to 6 pairs of ventral setae. Foretarsus of ♂ with segments I to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Entire surface with dense uniform pubescence.

Hind wing. Full and apparently functional.

Abdomen. Sterna covered with pubescence; sternum VI of ♂ with 1 pair of ambulatory

setae. Tergum VIII of ♀ with obtusely pointed apex (Fig. 201).

Female genitalia. Stylus dilated laterally, modified as described under subgenera.

*Discussion.* — *Amphasia* includes 2 subgenera: the nominate one with the single species *interstitialis* (Say), 1823, and *Pseudamphasia* with the single species *sericeus* (Harris), 1828. Both species are found in southeastern Canada and eastern United States. The close phylogenetic relationship of *Amphasia* and *Pseudamphasia* is shown by their synapomorphic character states of: elytron densely and uniformly pubescent; and stylus modified. The stylus in *Amphasia* is strongly dilated laterally and the apical segment has a serrate lateral margin with stout spines arising between the serrations (Fig. 234). The stylus in *Pseudamphasia* is less strongly modified being moderately dilated laterally and having on the apical segment (when not worn) a finely serrate lateral margin with very small spines arising from indentations between the serrations (Fig. 233). The elytral pubescence and modified styli, together with other characters discussed in the section on phylogeny of the genera and subgenera of Anisodactylina, suggest that *Amphasia* and *Pseudamphasia* are closely related sister groups.

While closely related, *Amphasia* and *Pseudamphasia* differ in enough characters normally conservative for groups of Anisodactylina to warrant separate subgeneric status: the stylus of *Pseudamphasia* is less derived than that of *Amphasia*; the valvifer in *Amphasia* (Fig. 229) is not vestigial while that of *Pseudamphasia* (Fig. 233) is; and the ligula of *Pseudamphasia* (Fig. 177) is expanded at the apex while that of *Amphasia* (Fig. 178) is not. Other characters less conservative for groups of Anisodactylina (and therefore of less subgeneric significance) separate the 2 subgenera: the frontal fovea of *Pseudamphasia* is large and shallow while that of most specimens of *Amphasia* is small and relatively deeper; and in *Pseudamphasia* the pronotal apex is less deeply emarginate, the elytral humerus more angulate, the body color different, and the setigerous punctures of the pronotum and elytron finer than in *Amphasia*.

### 33 subgenus *Pseudamphasia* Casey (Figs. 177, 233)

*Pseudamphasia* Casey, 1914: 195. [TYPE SPECIES: *Harpalus sericeus* Harris, 1828, by monotypy].

*Description.* — Body length 8.8 to 11.0 mm.

Color. Dorsum and venter piceous to black; frons with or without median rufous spot. Legs rufotestaceous to rufopiceous, femora darker in many specimens.

Head. Frons with fovea irregular, large, shallow, without clypeo-ocular prolongation; microsculpture of very prominent isodiametric mesh. Ligula with apex expanded laterally (Fig. 177); margin of apex with small tubercle medially in many specimens. Paraglossa subequal in length to ligula, narrowly rounded at apex (Fig. 177).

Thorax. Pronotum with microsculpture of prominent isodiametric mesh.

Elytron. Surface with dense, uniform pubescence (finer however than in *Amphasia*); humerus slightly angulate, without tooth, microsculpture of granulate slightly transversely stretched isodiametric mesh, more prominent in ♀; without iridescence.

Male genitalia. Median lobe with apex bent ventrad; ventral surface with prominent longitudinal striae. Internal sac with complex armature.

Female genitalia. Valvifer (Fig. 233) small, flat, vestigial; membranous except near lateral and mesal articulations; situated at base of stylus (Fig. 233) and difficult to find. Stylus (Fig. 233) moderately dilated laterally; lateral margin of apical segment finely serrate and with very small spines arising from indentations between fine serrations (serrations and spines much finer than those in *Amphasia*).

34 subgenus *Amphasia* Newman

(Figs. 178, 201, 229, 234)

*Amphasia* Newman, 1838: 388. [TYPE SPECIES: *Amphasia fulvicollis* Newman, 1838, by monotypy, = *interstitialis* Say, 1823].

*Description.* — Body length 8.5 to 10.2 mm.

Color. Dorsum with head and pronotum testaceous to rufotestaceous; elytron piceous and strongly iridescent. Venter various.

Head. Frons with fovea small, somewhat irregular in shape, in many specimens vaguely crescent shaped with both ends medially directed, in some specimens Y shaped with 2 forks directed posteriorly; microsculpture of isodiametric mesh, more prominent in ♀, obsolescent medially in many ♂♂. Ligula slender, not expanded at apex (Fig. 178). Paraglossa slightly longer than ligula, broad and obtuse at apex.

Thorax. Pronotum with microsculpture obsolescent or consisting of fine lines.

Elytron. Surface with dense, uniform pubescence; humerus rounded, without tooth; microsculpture of extremely dense, fine transverse lines, causing strong iridescence.

Male genitalia. Median lobe with apex bent sharply ventrad; sclerotized virga present on both sides of ostium. Everted internal sac with median field of prominent enlarged scales.

Female genitalia. Valvifer (Fig. 229) flattened, lightly sclerotized, with 2 to 5 distal setae. Stylus (Fig. 234) strongly dilated laterally; lateral margin of apical segment serrate and with short stout spines arising between serrations from dorsal side.

35 genus *Gynandromorphus* Dejean

(Figs. 197, 231)

*Gynandromorphus* Dejean, 1829: 186. [TYPE SPECIES: *Carabus etruscus* Ouensel, 1806: 212, by monotypy].

*Morphogynandrus* Carret, 1905: 122. [TYPE SPECIES: *Gynandromorphus peyroni* Carret, 1905, by monotypy].

*Description.* — Body length 10 to 11 mm. Body densely pubescent, form as in *Diachromus*.

Color. Dorsum tricolored; head and pronotum black; base of elytron rufotestaceous; apex of elytron violaceous brown. Venter black. Legs testaceous to rufotestaceous.

Head. Frontal fovea obsolescent, obscured by setigerous punctures. Mentum with prominent tooth. Mentum and submentum completely fused. Ligula very strongly expanded laterally at apex. Paraglossa slightly shorter than ligula.

Thorax. Pronotum cordate; lateral bead complete; apical bead present laterally; basal bead present at least laterally.

Legs. Foretibia with distal portion moderately expanded laterally; apical spur trifid. Hindtarsus with segment I shorter than II + III. Dorsum of all tarsi pubescent. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Foretarsus of ♀ with segment I enlarged and laterally expanded, remaining segments unmodified. Midtarsus of ♂ with segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Intervals moderately to densely pubescent; interval III without discernible dorsal setigerous puncture.

Abdomen. Sternum VI of ♂ with 1 or 2 pairs of ambulatory setae depending on species. Tergum VIII of ♀ with strongly angulate apex (Fig. 197).

Male genitalia. Median lobe of some specimens with distal portion deflected to the right; lacking apical disc.

Female genitalia. Valvifer (Fig. 231) moderately sclerotized, slightly convex; mesal margin somewhat membranous and indistinct; lateral margin distinct but with membranous lobe; distal portion with several prominent setae. Stylus with basal segment bearing 1 or 2 very small indistinct setae on lateral distal margin.

*Discussion.* — This genus contains 2 species: *etruscus* (Quensel), 1806 found in southern and middle Europe; and *peyroni* Carret, 1905 found in Syria and the Transcasian. Carret (1905) placed his new species in a new subgenus, *Morphogynandrus*, but subsequent authors have agreed that the characters cited by him are neither important nor stable enough to warrant separate subgeneric status for *peyroni*.

### 36 genus *Diachromus* Erichson (Figs. 204, 228)

*Diachromus* Erichson, 1837: 43. [TYPE SPECIES: *Carabus germanus* Linnaeus, 1758, by monotypy].

*Description.* — Body length 8 to 10 mm. Body convex, somewhat slender, pubescent. Color. Dorsum tricolored; head and base of elytron rufotestaceous; pronotum black, apex of elytron violaceous or bluish brown. Venter black.

Head. Frontal fovea obsolescent, obscured by setigerous punctures. Mentum with prominent tooth. Mentum and submentum completely fused. Ligula strongly expanded laterally at apex. Paraglossa approximately equal in length to ligula.

Thorax. Pronotum cordate; with seta located near middle of each lateral margin and additional seta situated by posterior angle; lateral bead complete; apical bead present only laterally; basal bead present but in many specimens obsolescent medially.

Legs. Foretibia with distal portion moderately expanded laterally; apical spur laterally expanded and somewhat spatulate. Hindtarsus with segment I shorter than II + III. Fore- and midtarsus of ♂ with apex of segment I (only extreme apical margin in midtarsus) and all of segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Intervals with dense, erect pubescence; interval III with discernible dorsal setigerous puncture near apical 1/4 in most specimens.

Abdomen. Sternum VI of ♂ with 2 pairs of ambulatory setae. Tergum VIII of ♀ with obtusely rounded apex (Fig. 204).

Male genitalia. Median lobe with median portion swollen in dorsal view; lacking apical disc.

Female genitalia. Valvifer (Fig. 228) moderately sclerotized; distal portion with several short setae. Stylus with basal segment bearing 1 or 2 short setae on apical lateral margin.

*Discussion.* — This genus contains only the species *germanus* (Linnaeus), 1758 found in England, southern Europe and around the Mediterranean. It is distinguished from all other Palearctic Anisodactylines by the additional seta present near the pronotal posterior angle.

### 37 genus *Dicheirus* Mannerheim

*Dicheirus* Mannerheim, 1843: 211. [TYPE SPECIES: *Harpalus dilatatus* Dejean, 1829, designated by Noonan (1968)].

*Description.* — Body length 5.3 to 14.5 mm. Body covered with setigerous punctures. Color. Rufous to black depending on body part and on species; without metallic tinge.

Head. Clypeus with 1 to 4 setigerous punctures at each outer distal angle. Frontal fovea obsolescent. Mentum with or without tooth. Mentum and submentum completely fused. Ligula strongly expanded laterally at apex. Paraglossa slightly longer than ligula; with very

fine, short hairs on sides, apex, and dorsum (evident at magnifications of 120X or more).

Thorax. Pronotum with lateral bead complete; apical bead absent; basal bead present but in many specimens interrupted medially.

Legs. Foretibia with distal portion strongly expanded laterally; apical spur strongly trifid. Hindtarsus with segment I shorter than II + III. Dorsum of all tarsi with sparse to dense pubescence. Foretarsus of ♂ (except some specimens of *dilatatus angulatus*) with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with or without some segments laterally expanded and spongy pubescent beneath.

Elytron. Intervals II to VII, II to VIII, or II to IX, depending on species, with 2 rows of setigerous punctures; outer intervals with irregular row(s) of setigerous punctures; interval III without apparent dorsal setigerous puncture.

Hind wing. Full and apparently functional or vestigial depending on species.

Abdomen. Sternum VI of ♂ with 1 or 2 pairs of ambulatory setae in most specimens. Tergum VIII of ♀ various.

Male genitalia. Median lobe without apical disc; membranous area of dorsum elongate and extended nearly to basal bulb in all species except *obtus*; entire shaft twisted in *piceus*, not twisted in other species. Internal sac without armature.

Female genitalia. Valvifer various according to species. Stylus with basal segment bearing 2 to 4 prominent long setae on apical lateral margin; apical segment in all species except *obtus* with several setae at base.

*Discussion.* — The 5 species of this genus, all found in the western United States or southwestern Canada, are: *brunneus* (Dejean), 1829; *dilatatus* (Dejean), 1829; *obtus* LeConte, 1851; *piceus* (Menetries), 1844; and *strenuus* (Horn), 1868. Noonan (1968) revised the genus and provided a key to the species, and Lindroth (1968) keyed out the northern forms. *Dicheirus* has been placed in *Anisodactylus* by some past authors but warrants separate status due to the total absence of an apical bead on the pronotum (Lindroth, 1968) and the densely pubescent elytra.

## PHYLOGENY

### Introduction

Hennig (1966) provided principles for reconstructing phylogenies of extant organisms, leading to renewed interest in methods for elucidating phylogenies. Four workers have produced major papers discussing, variously modifying, and utilizing Hennig's principles in reconstructing phylogenies of insect groups: Brundin (1966) on midges of the South Hemisphere; Erwin (1970) on species of *Brachinus* (Coleoptera: Carabidae); Donald Robert Whitehead (1972) on species of *Schizogenius* (Coleoptera: Carabidae); and Griffiths (1971) on Cyclorrhapha (Diptera).

Seven workers have published important papers on theoretical aspects of phylogenetic principles. Hull (1970) and Mayr (1969) reviewed the principles of Hennig and the broadened phylogenetic principles enunciated by Brundin (1966) and discussed other systems for constructing classifications. Darlington (1970) pointed out practical problems concerning the principles of Hennig and Brundin. In turn, Nelson (1971a) defended Hennig and Brundin's ideas and offered arguments for accepting dichotomous evolution. Darlington (1972) replied to Nelson's comments and asked for clarification of Hennig and Brundin's principles. Brundin (1972) defended his and Hennig's ideas and criticized Darlington's (1970) paper. And Ashlock (1971), Colless (1972), and Nelson (1971b) dealt with definitions of monophyly, paraphyly, and polyphyly.

### Phylogenetic Methods

From the many ideas and models discussed by the above authors I selected the following methodological principles for constructing Anisodactylinae phylogenies: (1) assumption of dichotomous cleavage of each ancestral taxon to produce 2 sister taxa; (2) determination of relationships by synapomorphy; (3) clarification of relationships by chorology.

Darlington (1970) pointed out that dichotomous cleavage has not been proven for the evolution of species, is in fact unlikely, and is an oversimplification of what actually occurs in nature. These points may well be true. However, available data may not clearly indicate whether a species or higher taxon simultaneously split into 2, 3, 4 or whatever number of descendants. Therefore, I believe dichotomous cleavage, used as a methodological model, is a legitimate assumption that allows reconstructing an orderly phylogeny in accord with the principle of parsimony.

Hennig (1966) and Brundin (1966) asserted that sister taxa should be given equal rank. This stems in part from their belief that dichotomous evolution is the actual way in which evolution proceeds rather than being simply a convenient model by which to construct orderly phylogenies. Giving equal rank to sister taxa would lead to excessive splitting of groups and require additional supra-specific categories. Therefore, I have not always given equal rank to sister taxa in this paper.

The logical first step in reconstructing a phylogeny of extant organisms is to determine which of them are most closely related on the basis of synapomorphy and chorology. Most extant taxa can be grouped into pairs (sister taxa) the members of which are more closely related to each other than to any other extant taxon.

Some taxa may appear to lack sister taxa because: (1) the sister taxa are extant but not yet collected; (2) the sister taxa are extinct; (3) three or more taxa are equally related to each other due to simultaneous evolution from the same ancestor. The first two possibilities can be evaluated by a specialist familiar with how well the group in question has been collected and how common extinctions appear to be in the group. The third possibility can be evaluated by determining if 3 or more taxa are as closely related to one another as any 2 of them are to each other. If 3 or more taxa do indeed seem so related, then the phylogeny should be drawn to reflect this, with an ancestral taxon shown as simultaneously dividing into 3 or more taxa. Unpaired taxa which have resulted from the first 3 possibilities should be connected to the phylogeny by dotted lines, and their most probable relationship to paired or sister taxa in the group discussed.

Determination of plesiomorphic and apomorphic character states is essential for elucidation of sister taxa. Plesiomorphic character states are those which evolved in a relatively early ancestor of a group of taxa. The plesiomorphic character states may be retained by various extant taxa and therefore may characterize both closely and distantly related taxa. Apomorphic character states are those which evolved in a more recent ancestor of a group of taxa and consequently are more likely to be restricted to a single taxon or to a single monophyletic group of taxa. Therefore, the use of apomorphic character states as indicators of relationship is less likely to result in distantly related forms being mistakenly treated as closely related.

When fossils are scanty or absent (as in Carabidae), the best method of distinguishing apomorphic character states from plesiomorphic ones is to analyze morphoclines (transformation series) as suggested by Maslin (1952). If such morphoclines are not found, one must assume that character states widespread among diverse groups are plesiomorphic while those restricted to only a few groups are apomorphic or less likely are relictual. The latter possibility can be evaluated by a worker familiar with the group in question. Lastly, in some instances character states may correlate with other character states whose value is already

known.

The chorological method may help in elucidating relationships by examining extant distribution patterns to determine probable evolutionary histories. Also used are data from such topics as: past floras and faunas; past climates; and past continental drift. Data on past floras, faunas, and climates help in elucidating relationships among species, and together with data on past continental drift may help in determining relationships among supra-specific taxa.

Forms regarded as "sister" taxa may actually not have evolved from an immediate common ancestor but rather be the sole survivors of once extensive sister groups of taxa. Such a hypothetical instance is illustrated in Fig. 244 in which "G", "I" and "C" are the only extant forms of a lineage. The taxa "G" and "I" are the survivors of the sister groups "F", "G" and "H", "I" and share several apomorphic character states which evolved in the extinct taxon "B". A worker reconstructing the phylogeny of "G", "I", and "C" might very likely draw the reconstructed phylogeny as in Fig. 245 thus treating "G" and "I" as sister taxa and as older than they are. A reconstructed phylogeny can only indicate the most probable maximum age of a taxon. Therefore, it often is not correct to determine the age of a taxon by noting where it branches off from the main part of a phylogenetic diagram.

### Phylogeny and Chorology

Because several lineages within the subtribe Anisodactylina have no apparent synapomorphies, I used chorological data in assembling the phylogeny. Postulated past movements of continents are especially useful in determining the sequence of development of various lineages and supra-specific taxa of the subtribe Anisodactylina whose origin I presume was in late Jurassic or very early Cretaceous. My primary reference for past positions of continents was Dietz and Holden (1970), the only synthesis I found with clear maps of past positions of all continents. Other sources consulted to confirm (or sometimes slightly modify) conclusions by Dietz and Holden were: Smith and Hallam (1970); Malfait and Dinkleman (1972), and Morgan et al (1969).

Many previous biogeographers who worked primarily with land vertebrates have felt either: that distribution patterns disproved or at least did not suggest continental drift (Matthew, 1915; Darlington, 1957; Simpson, 1962); or that such drift was limited (Darlington, 1965). The present distribution of continents is such that the Northern Hemisphere contains about twice as much land as does the Southern (Darlington, 1957). And the current arrangement of continents is such that "north of the tropics, there are large areas which are nearly connected; within the tropics, large areas which are separated from each other; and south of the tropics, smaller areas which are very widely separated from each other" (Darlington, 1957, p. 3). Matthew (1915) proposed: that the North temperate Region has been the main center of evolution and dispersal of land vertebrates because of past climatic fluctuations; and that no continental drift or former land bridges were necessary to explain contemporary vertebrate distribution. Darlington (1957; 1959) discussed Matthew's ideas and presented arguments for the Old World Tropics as the main center of land vertebrate evolution and dispersal. The disjunct southern land areas were considered primarily as recipients of a stream of animals evolving in and dispersing from larger northern areas (Darwin, 1856; Darlington, 1957, 1959, and especially 1965).

It has been accepted by many workers that the general pattern of land vertebrate evolution has been evolution of dominant forms in northern areas (whether tropical or temperate) and subsequent spread to other lands such as those of the Southern Hemisphere. Darlington (1957, 1959, 1965) presented the following points in support of a northern origin of land vertebrates. As a general rule, continental faunas are superior to and can displace island ones.



And faunas evolved from large areas can usually supplant or out complete faunas evolved from small areas. Dominant groups are the most likely ones to disperse. The Old World Tropics constitute a large area with favorable climate. The general pattern of evolution of land vertebrates has been evolution of dominant groups in the Old World Tropics and subsequent spread to northern and southern lands.

I agree with Darlington that faunas evolving in large areas can usually supplant those evolving in smaller ones, that dominant forms do show a tendency to evolve in areas with favorable climate, and indeed that the evolution of land vertebrates *may* have taken place primarily in northern areas. However, Fooden (1972) convincingly postulated an origin of mammals on Pangaea and correlated current distributions with past episodes of continental drift. And that some or many land vertebrates *may* have evolved in northern areas does not mean insects must also have done so.

More important, the thesis of evolution in northern areas and flow of dominant animals to disjunct southern lands is dependent on the thesis of permanence of continents. Geologists now agree that continents have not always had their present positions and in fact have moved quite freely over the surface of the earth. Data supplied by many workers including the geologists cited earlier indicate that approximately 200 million years ago all continents were grouped into a single supercontinent, "Pangaea". During much of the Mesozoic, Australia, New Zealand, New Guinea, and Antarctica constituted a single landmass while Africa and South America were also joined. The Australia-Antarctica landmass, the South America-Africa landmass, and India constituted during part of Mesozoic at first a single joined landmass termed "Gondwanaland" and later (except for India) were closely associated for a long period of time (Figs. 247, 250).

The existence of a large unit of closely situated or joined landmasses satisfies Darlington's requirement of large land area for evolution of dominant forms. And the past positions of these landmasses suggest favorable climate, thus satisfying Darlington's second criterion. The area-climate-evolution hypothesis of Darlington thus readily permits and even strongly suggests that Gondwanaland may have been an important center of evolution during the Mesozoic. The possible lack of evidence for a Gondwanaland center of origin for many land vertebrates may be due either to evolution of such groups taking place after the continents had nearly or completely reached their present position or to the early fossil record being incomplete. Each group of animals or plants must be carefully examined to determine if its present distribution and fossil record (if present) suggest evolution and dispersal from Gondwanaland. This is especially true of insects!

Several biogeographers have considered continental drift in explaining contemporary distribution of groups of insects. Since I have found the theory of continental drift useful in explaining the present distribution of Anisodactylina, works of 4 of these biogeographers will be discussed to place my own work in a frame of reference. As far as I know, Jeannel was the first biogeographer to employ continental drift theory to explain present distributions of Carabidae. (He also used continental drift theory to explain distributions of other groups of organisms.) Three of his works will be reviewed here. Other works reviewed here are by Ball, Brundin, and Darlington.

In 1938 Jeannel published a revision of Migadopini, a primitive group of Carabidae found in now disjunct areas of the southern hemisphere. Jeannel listed 5 lineages within Migadopini: (1) a primitive Australian-New Zealand lineage comprised of three genera and found in Australia, New Zealand, and the Auckland Islands; (2) an Australian lineage confined to Australia and Tasmania; (3) a derived lineage endemic to New Zealand; (4) a South American lineage containing species with harpaline facies; and (5) a monotypic, phylogenetically isolated Chilean lineage. According to Jeannel, the contemporary distribution of Migadopini

in widely disjunct austral regions is explained by these regions once being grouped together into a single landmass.

In his classic book on southern hemisphere biogeography Darlington (1965) pointed out that: (1) the tribe Migadopini contains winged species in both Australia and Chile; (2) the tribe has forms occurring at warm temperate or subtropical localities; (3) existing genera are very diverse, suggesting they are products of a complex ecologic as well as geographic radiation rather than simple spread from an antarctic center and; (4) closest relatives of tribe are probably the north temperate Elaphrini. He concluded (p. 37) from these 4 points "that the ancestor of the Migadopini was winged, that it may have lived in or dispersed through relatively warm climates, that the history of the tribe has been complex, and that a common ancestor of this tribe and the Elaphrini crossed the tropics a long time ago. These details do not disprove an antarctic origin of the Migadopini but do suggest other possibilities." Elsewhere (pp. 47-50) Darlington suggested for Migadopini, Broscini, Trechini, and *Bembidion* (latter 3 groups are also Carabidae) an apparent dispersal cycle of: "rise on the large land masses in the Northern Hemisphere, or possibly in the tropics; dispersal southward into southern America and southern Australia by separate routes, and to New Zealand probably from Australia; disappearance of the tropical or tropics-crossing forms, leaving an amphitropical pattern; and finally disappearance from the Northern Hemisphere, leaving survivors on the three main pieces of land in the southern cold-temperate zone. (Other groups might disappear in the Southern Hemisphere and survive only in the Northern.)"

Brundin (1966 pp. 63-64) disputed Darlington's 4 points (and indirectly the suggested dispersal cycle) by stating: (1) presence of winged groups does not disprove past evolution on Gondwanaland nor spread from that landmass; (2) subgroups of Migadopini need not be expected to all be adapted to only cold environments; (3) spread from an antarctic center need not be simple; (4) possible relationship to the more apomorphic Elaphrini suggests "the apomorphic sister species of the migadopid ancestor migrated northwards and became the ancestor of Elaphrini".

Without fossil evidence it will never be possible to *prove* the origin of Migadopini nor of other groups of Carabidae. One can only speak in terms of probability. The dispersal cycle suggested by Darlington (1965) may be true for certain possibly more recently evolved groups of Carabidae such as *Bembidion*. However, for older and exclusively austral groups such as Migadopini this suggested dispersal cycle requires more assumptions and is therefore less likely than the origin suggested by Jeannel. Further, the dispersal cycle suggested by Darlington assumes "rise on the large land masses in the Northern Hemisphere, or possibly in the tropics"; Gondwanaland was such a landmass, but in the Southern Hemisphere.

In his 1940 revision of *Calosoma* Jeannel provided an extensive discussion of chorology and evolution. He provided maps of past continental drift accepted by him and explained present distribution of *Calosoma* partly on the basis of evolution in and dispersal from Gondwanaland. Certain land arrangements and timings of continental movements postulated by Jeannel are today not accepted by geologists. And the taxonomic work done by Jeannel is weak in some aspects. However, his use of information concerning past continental movements to explain contemporary distribution patterns must be regarded as a pioneering effort.

Jeannel (1942b) produced a biogeography book dealing primarily with the origins and dispersal of insects. Hypotheses about groups were based largely on postulated past continental movements which were illustrated in 8 plates covering the upper Carboniferous to Pliocene. In his eagerness to explain extant insect distributions by continental drift, Jeannel unfortunately formed some taxonomic groups in such a way that they would "fit" continental drift. In his review of the book Darlington (1949) pointed out that it contributed much original information on evolution and on past dispersals of some groups but suffered from

being (p. 345) "a succession of dogmatic statements with no distinction between fact and opinion". Jeannel's failure to consider alternative explanations for extant insect distributions greatly weakens the usefulness of the book. Nevertheless, his work is important to biogeographers since: (1) it is one of the few major works treating insect biogeography in detail; (2) Jeannel did accept continental drift long before many other biogeographers in Europe and North America; (3) information and theories presented in the book should stimulate other biogeographers.

Ball (1956) briefly reviewed the classification and distribution of Broscini (Carabidae) at a time when neither he nor most geologists accepted continental drift. He recognized 3 subtribes: (1) *Barypina*, restricted to southern South America; (2) *Creobina* found in southern South America and western Australia; (3) *Broscina* with center of abundance in the eastern Palearctic but found also in New Zealand, Australia, the Nearctic and the northern fringe of the Oriental Region. Ball concluded that ancestral stocks of the former 2 subtribes possibly arose in the southern hemisphere and reached South America by way of a southern route. He noted that geological data (in 1956) did not support a direct land connection between South America, Antarctica, New Zealand, and Australia. Therefore, he concluded (p. 46) it was impossible to state whether invasion of South America took place "by dispersal from island to island or by way of a direct land connection".

According to Ball (p. 47) the subtribe *Broscina* most likely "arose in the southeastern Palearctic or in Australia and dispersed from either of these centers possibly by way of what is now the Indo-Australian Archipelago." This is in disagreement with Britton's (1949) suggestion that the tribe Broscini originated on Cretaceous Southern Hemisphere landmasses, probably reached South America by southern land connections, and later spread from there through Africa to Eurasia. Contemporary continental drift theory connects South America, Africa, Australia, New Zealand, New Guinea, and Antarctica during early Mesozoic but does not connect Australia to Asia via the current Indo-Australian Archipelago until Tertiary. Thus, as Britton suggested, dispersal via the Indo-Australian Archipelago may be improbable since Broscines could not have reached Asia via this route early enough to account for the considerable diversification of the Palearctic genera and species.

Ball pointed out that if we knew more about continental drift, we would know more about the most probable dispersal times and routes of Broscines. In view of currently accepted continental drift theory, it seems more probable to me that the ancestor of the subtribe *Broscina* reached either the South American or African portion of the combined South America-Africa landmass via direct land connections or across narrow water gaps in the Jurassic or early Cretaceous and passed through Africa into the Palearctic. Then the ancestor died out in Africa (and also South America if it ever reached that continent). This postulated dispersal provides adequate time for extensive diversification of genera and species in the Palearctic Region. Later, when the Bering Land Bridge was exposed in the Tertiary, members of the subtribe could have crossed into North America.

Probably the most discussed recent work correlating insect distribution with continental drift is Brundin's 1966 book. In this work Brundin summarized and extended the phylogenetic principles of Hennig (1966) and then employed them in his monograph of the Chironomid subfamilies Podonominae, Aphroteniinae, and the austral Heptagyiinae. He also discussed transantarctic relationships of other groups of organisms and explained these relationships in part by continental drift.

Brundin's postulated history of the midges seems possible to me except perhaps that several sister species are found on widely disjunct lands. One or both of the following possibilities may explain this occurrence of sister species on widely disjunct lands: (1) the sister species recognized by Brundin may each actually be the sole survivor of species groups dating

back to the Mesozoic; (2) the sister species may have dispersed via Antarctica during the Tertiary. Dispersal across present water gaps seems unlikely to me because of the danger of desiccation during such dispersal. I am aware that chironomids are frequently taken by aerial nets but know of no studies showing that they are alive at the moment of capture.

### Phylogeny of the genera and subgenera of the Anisodactylina.

Table 2 (p. 429) indicates the plesiomorphic and apomorphic states of each character employed in the reconstructed phylogeny of Anisodactylina presented in Figs. 240, 241. Unless otherwise indicated in the text, plesiomorphic and apomorphic states are determined by their distribution among supra-specific taxa of Anisodactylina or other Carabidae.

The extant supra-specific taxa of Anisodactylina can be grouped into 2 main branches: (1) the Notiobioid main branch with the mentum and submentum separated by a complete transverse suture (except *Anisostichus*) and (2) the Anisodactyloid main branch with the mentum and submentum fused only laterally or fused completely. The first group represents the plesiomorphic state in Anisodactylina since as far as I know the mentum and submentum are separated by a complete transverse suture in most other tribes of Carabidae and in all subtribes of Harpalina except the subtribe Bradycellina. Within this latter subtribe the mentum and submentum are fused in species of a few genera but are separated by a complete transverse suture in all other genera. The Anisodactyloid main branch in turn possesses a character state clearly apomorphic within Harpalini and within the subtribe Anisodactylina.

The Australian Region (except for New Guinea which contains 2 species of *Chydaeus* derived from stocks in Asia) lacks members of the Anisodactyloid main branch (Fig. 246) and contains only members of the relatively more plesiomorphic Notiobioid main branch. Moreover, Notiobioids found in the Australian Region are relatively plesiomorphic compared with Notiobioids found in other parts of the world.

The most probable explanation for the absence of apomorphic forms in the Australian Region is that Anisodactylina arose on the combined landmass (hereafter termed Australia-Antarctica) of Australia, Antarctica, New Guinea, and New Zealand, spread to other regions and evolved more apomorphic forms in these other areas.

The Australia-Antarctica landmass was separated from the northern continents by the end of the Triassic (Dietz and Holden, 1970). This might suggest that the ancestor of Anisodactylina arose during the Triassic. However, beetles apparently arose in the Permian (Crowson, 1955), and the Harpalini are moderately apomorphic within the family Carabidae. Therefore, it is more likely that the ancestor of the subtribe arose in Australia-Antarctica during very late Jurassic or early Cretaceous, and then members later crossed the narrow water gap to the combined continents (hereafter termed South America-Africa) of South America and Africa (Figs. 247, 248).

Darlington (1965) pointed out that southern Australia was non glaciated and possibly warmer than now but not tropical from Permian to Tertiary, when it became cooler. New Guinea and the northern edge of Australia (Darlington, 1965) are and probably long have been tropical, and between tropical and south temperate areas of Australia there now is and probably long has been a broad barrier of more or less drier country. Darlington further stated that very few Triassic and Jurassic plants have been so far found on the main part of Antarctica, but a moderately diverse Jurassic flora has been found on the Antarctic Peninsula. Lower Triassic fossil beds along the southwest coast of Antarctica have yielded labyrinthodont amphibians, thecodont reptiles, and therapsid reptiles (Elliot et al, 1970; Fooden, 1972; Kitching et al, 1972). And during Jurassic and early Cretaceous (Dietz and Holden, 1970) the Antarctica portion of Australia-Antarctica was located further north than at present (Fig. 248). The presence of Jurassic fossils on Antarctica and its more northerly

location suggest that this area had a much milder climate than at present. This would permit evolution and migration of Anisodactylina along at least the northern edge of Antarctica. Most of the taxa of Anisodactylina contain species primarily adapted to temperate conditions. And 4 of the 5 presumably oldest groups, (*Allocinopus*, *Triplosarus*, *Hypharpax*, and *Cenogmus*) are primarily centered in temperate areas. Thus, the ancestor of Anisodactylina probably was adapted to temperate or warm temperate conditions.

The endemic New Zealand genus *Allocinopus* does not appear closely related to any other extant groups of the Notiobioid main branch and therefore is connected by a dotted line to the phylogenetic diagram in Fig. 240. Most likely, the ancestor of *Allocinopus* became isolated in New Zealand when this group of islands became separated from Australia and Antarctica. Smith and Hallam (1970) date such separation from between middle Jurassic to middle Cretaceous while Dietz and Holden (1970) date it from early Tertiary. The distinctiveness of *Allocinopus*, character variation demonstrated by its species, and the distinctiveness of *Triplosarus* (the other endemic New Zealand genus) suggest separation in the Cretaceous.

The ancestor of *Allocinopus* may have given rise to a group of genera which became extinct except for *Allocinopus*. Or the ancestor may have been a member of a lineage once widespread on Australia and Antarctica. Australia and New Zealand are moderately well collected in terms of Carabidae, and therefore it is unlikely that an extant sister genus will be found. *Allocinopus* appears to be a phylogenetic relict.

The ancestor of Anisodactylina which presumably arose in temperate or warm temperate areas of Australia-Antarctica during late Jurassic or early Cretaceous, soon gave rise to the *Notiobia* and *Cenogmus* branches. The first branch remained essentially unchanged from the ancestral condition, but the second or *Cenogmus* branch gained the apomorphic feature of extra setae on the abdominal sterna. Part of this second branch migrated to the New Zealand portion of Australia-Antarctica, became isolated when New Zealand became separated, and eventually evolved into the endemic genus *Triplosarus*. Smith and Hallam, 1970 stated that such separation probably took place between middle Jurassic and middle Cretaceous, but Dietz and Holden (1970) date separation from early Tertiary. The distinctiveness of *Triplosarus* and of the other endemic New Zealand genus, *Allocinopus*, suggests separation in the Cretaceous. The Australian portion of the *Cenogmus* branch subsequently divided into the *Hypharpax* sub-branch, which ultimately gave rise to the genus *Hypharpax*, and into the *Cenogmus* sub-branch. A member of the *Cenogmus* sub-branch crossed the water gap (Fig. 247) between Australia-Antarctica and South America-Africa. Most likely it never reached the South American part of the landmass but became established in Africa and there evolved into the genus *Crasodactylus*. This genus subsequently spread to India but was displaced from most of tropical Africa by members of the more apomorphic Anisodactyloid main branch.

An alternative possibility for the evolution and dispersal of the *Cenogmus* sub-branch (suggested in part by G. E. Ball, personal communication) is as follows. The genus *Hypharpax* does not possess as many apomorphic character states as do *Crasodactylus* and *Cenogmus*. Acquisition of apomorphic features takes time, and therefore the latter two genera are probably much older than *Hypharpax*. Both *Crasodactylus* and *Cenogmus* evolved on and were at first present over much of Australia-Antarctica (minus the already split off New Zealand). As the landmass split up, both genera remained on the Australian portion and did not cross the water gap to South America or Africa. When the Indo-Australian Archipelago was formed during the Tertiary, *Crasodactylus* used this Archipelago to disperse to tropical Asia. The genus subsequently spread across tropical Asia to Africa and therefore is only a recent arrival there. The more recently evolved genus *Hy-*

*pharpax* ultimately displaced *Crasodactylus* from Australia, the Indo-Australian Archipelago, and tropical Asia in a manner similar to the "Taxon Cycle" suggested for certain ants by Wilson (1961).

This alternative sequence of evolution and dispersal of the *Cenogmus* sub-branch seems less likely to me than the evolution of *Crasodactylus* in Africa itself. Evolution of *Crasodactylus* in Australia and dispersal across the Indo-Australian Archipelago requires crossing of many water barriers, while evolution of *Crasodactylus* in Africa requires crossing only one water barrier. At the moment there is not sufficient ecological information on the species of *Crasodactylus* and *Hypharpax* to determine if they inhabit similar habitats or if they would have competed with each other in the past if species ranges overlapped. If the assumption is made that *Hypharpax* species did compete with and displace species of *Crasodactylus* in the Tertiary, then at least some of the islands in the Indo-Australian Archipelago might be expected to contain relict populations of *Crasodactylus*. To my knowledge, none do so. And *Crasodactylus* dispersing through tropical Asia to Africa would probably have had to compete with members of the more apomorphic Anisodactyloid branch already in Asia or just dispersing to Asia from western Eurasia and Africa.

These points do not disprove the alternative possibility for the evolution and dispersal of the *Cenogmus* sub-branch. It is possible for groups to cross more than one water barrier. Extinction of groups in areas through which they dispersed is not impossible and in fact was postulated by me earlier in this paper in discussing the dispersal of Broscine carabids. And species of *Crasodactylus* and of the Anisodactyloid main branch may have occupied quite different niches and not been in competition. Nevertheless, the mechanism for evolution and dispersal of the *Cenogmus* sub-branch postulated by me is more parsimonious than the alternative one.

The *Notiobia* branch on Australia-Antarctica was originally characterized by features ancestral for the subtribe. It subsequently split into the *Notiobia* sub-branch which retained ancestral features and into the *Gnathaphanus* sub-branch, which had the apomorphic feature of third elytral interval with few to many dorsal setigerous punctures.

A member of the plesiomorphic *Notiobia* sub-branch then crossed (Fig. 248) the water gap between Australia-Antarctica and South America-Africa. It probably radiated and gave rise to a now largely extinct complex of groups which dispersed across South America-Africa and reached temperate Eurasia. The past occurrence of such a complex of groups is suggested by the presence of the genus *Scybalicus* in England, Europe, northern Africa, and Asia Minor. This genus belongs to the Notiobioid main branch but is the only one having the apomorphic character state of body densely pubescent. It is not closely related to other taxa of the Notiobioid main branch, which suggests past extinctions of its sister group and other relatives. In Fig. 240 the genus is shown to evolve after the South American groups of the Notiobioid main branch. This is because the South American groups presumably arose in temperate southern South America from an ancestor similar to that of the *Notiobia* sub-branch in temperate portions of Australia-Antarctica. *Scybalicus* presumably was derived from a stock which crossed the tropics of at least Africa, died out in these tropics, and became restricted to the areas now occupied by the genus. However, firm evidence as to time of origin of *Scybalicus* is lacking, and the genus may have arisen before or concurrently with the South American groups.

A member of the postulated complex of Notiobioid groups became established in temperate southern South America and ultimately diverged into the *Criniventer* and *Notiobia* stocks. The former stock possessed the apomorphic features indicated in Fig. 240 and ultimately diverged into the monotypic genera *Criniventer* and *Pseudanisotarsus*. The *Notiobia* stock retained those features found in the Australia-Antarctica ancestor but acquired the

apomorphic feature of female valvifer weakly sclerotized and with membranous or semi-membranous distal lateral margin. The *Notiobia* stock then split into the relatively plesiomorphic *Notiobia* lineage and into the more apomorphic *Anisostichus* lineage characterized by apomorphic features of mentum and submentum fused, and third elytral interval with row of dorsal setigerous punctures.

The presence or absence of a complete transverse suture dividing the mentum and submentum is elsewhere in this discussion treated as a fundamental character separating Anisodactylina into 2 main branches of evolution. However, the distribution of characters within species of *Anisostichus* and within the 3 sub-genera of the *Notiobia* lineage suggest that *Anisostichus* arose from *Notiobia* stock and that the fusion of mentum and submentum is an example of parallelism.

The extant members of the *Notiobia* stock (including *Anisostichus*) all possess a prominent mental tooth (except for a few apomorphic species of *Anisotarsus* that have secondarily lost this tooth) and have a weakly sclerotized valvifer in which the distal lateral margin is membranous. A mental tooth is a plesiomorphic character state while the type of valvifer described above is an apomorphic character state. The extant New World species of the subgenera *Notiobia* and *Anisotarsus* have, except for a few species of *Notiobia*, the dorsal membranous area of the median lobe elongate and reaching the basal bulb. The length of this membranous area is varied within the sub-genus *Diatypus* and Australian species of *Anisotarsus*. The character state of an elongate dorsal membranous area on the median lobe is thus widespread among the extant species of the genus *Notiobia* and therefore probably ancestral.

As regards *Anisostichus*, in the species *posticus* and *octopunctatus* the mentum and submentum are fused but the suture formerly separating them is still indicated by a moderately deep transverse groove; and the dorsal membranous area of the median lobe is elongate and reaches the basal bulb. In the remaining 2 species, *amoenus* and *laevis*, the former suture between the mentum and submentum is represented at most by a shallow and difficult to discern transverse impression; and the dorsal membranous area of the median lobe is short and does not even approach the basal bulb. The species *octopunctatus* and *posticus* have a type of mentum and submentum intermediate between the apomorphic form described for *amoenus* and *laevis* and the plesiomorphic form found in all *Notiobia*. And the elongate dorsal membranous area of the median lobe represents the plesiomorphic character state possessed by the assumed common ancestor of the *Anisostichus* and *Notiobia* lineages. In addition, both these lineages possess the apomorphic feature of a weakly sclerotized valvifer with membranous distal lateral margin.

The distribution of the 4 species of *Anisostichus* provides clues as to the geographical origin of this group. The species *octopunctatus* and *posticus*, here regarded as relatively primitive forms in the genus, are found in southcentral and southeastern South America (*octopunctatus* apparently being restricted to the southeastern portion). The more derived forms, *amoenus* and *laevis*, are common in the Chilean region, although *laevis* occurs elsewhere in South America. The genus *Notiobia* is apparently absent from the Chilean region. These facts suggest that *Anisostichus* evolved in the southeastern (or less likely the south-central) part of South America where the primitive species *octopunctatus* and *posticus* still survive. It then spread into the Chilean region where the more derived species *amoenus* and *laevis* arose.

Evolution of the *Anisostichus* lineage took place during the Cretaceous when South America and Africa were joined along their present northern coastlines. Evolution of the lineage could not have taken place after late Cretaceous. The two continents were by then completely separate, and the *Diatypus* group which evolved after the *Anisostichus* lineage

could not have reached Africa unless this continent was still attached to South America or at most separated by only a narrow band of ocean.

I think the sequence of evolution outlined above for the *Anisostichus* lineage is the most probable one, but I cannot conclusively prove that *Anisostichus* does not belong to the Anisodactyloid main branch. However, I can state that if *Anisostichus* were so placed, it would have no sister group since it has no close relationships to supra-specific taxa in that main branch.

The *Notiobia* lineage in temperate southern South America soon split into tropical adapted and temperate adapted sublineages. The tropical adapted sublineage possessed the apomorphic character states of: adaptations for tropical habitats; gena narrow; eye large and bulging; and clypeo-ocular prolongation present, at least in some species. Maps provided by Dietz and Holden (1970) show that the northern parts of South America and Africa were located near the present day equator during the late Jurassic and early Cretaceous (Fig. 249). Therefore, the northern parts of these two continents probably then had a tropical climate. The tropical adapted sublineage spread throughout the tropical portions of northern South America and crossed into the tropical portions of northern Africa via the northern connection of the two continents (Fig. 249).

The temperate adapted sublineage retained the plesiomorphic character states of: adaptations for temperate habitats; gena wide; eye size normal; and clypeo-ocular prolongation absent. This sublineage was not able to move into the northern tropical portion of South America which was still attached to or very close to Africa in the Cretaceous, and consequently it did not reach Africa.

The tropical adapted sublineage split with the rupture of Africa and South America. The stock thus isolated in Africa gave rise to the subgenus *Diatypus* while the stock isolated in South America gave rise to the subgenus *Notiobia*. A continental connection remained between Africa and South America until at least middle Cretaceous (Smith and Hallam, 1970), and, presumably, for some time after the rupture of this connection, interchange remained possible across the narrow band of sea separating Africa and South America. Thus, the separation of stocks in Africa and South America probably dates from early Tertiary.

The origins of *Notiobia* and *Diatypus* postulated above may be objectionable to workers who believe subgenera must always be very recently evolved entities. Only scanty fossil data is available for Carabidae. But I expect that as fossil data are gathered, it will become apparent that many specific and supra-specific taxa of Carabidae are quite old. For example, Erwin (1971) reported that a fossil Upper Oligocene or Lower Miocene tachyine carabid belongs to an extant genus and represents a species (p. 234) "hardly different from extant species now living in cloud forests of eastern Mexico (Tamps.) and other Neotropical and Nearctic species I have studied." Erwin concluded (p. 236) that "The Mexican Amber specimen represents a species of *Polyderis*, an extant group of tachyine beetles world-wide in distribution. The similarity of characteristics with present species in the same area shows that externally, at least, characteristics have hardly changed in 30 million years." A more recent time than early Tertiary for separation of the ancestors of *Notiobia* and *Diatypus* is unlikely. Such a more recent time would require invoking a whole series of postulates concerning migration across northern temperate zones and subsequent extinction in these zones. In addition, an early separation of the ancestors of *Notiobia* and *Diatypus* may be indicated by the relative degree of diversification demonstrated by described species of *Diatypus*.

Species of the subgenus *Diatypus* are placed in 2 species groups based on the structure of the ligula. The first group (formerly termed subgenus *Diatypus*) consists of species retaining the plesiomorphic state of slender ligula. The second group (formerly termed subgenus *Para-*



*diatypus*) consists of those species with an apomorphic type of ligula bearing a laterally expanded apex. A few of the species of this group have the suture separating the mentum and submentum reduced and seemingly independently evolving towards the fused condition found in the Anisodactyloid main branch. The subgenus *Notiobia* is concentrated in tropical South America, and most of its species are probably undescribed; a study of the South American forms may also demonstrate considerable diversification within this subgenus.

The temperate adapted sublineage, which never reached Africa because of the tropical climate in the northern portion of South America, gave rise to the subgenus *Anisotarsus*. This subgenus is composed of 2 species groups: the "*Anisotarsus*" group consisting of all species found in the New World; and the "*Diaphoromerus*" group consisting of all species occurring in the Australian Region. The only appreciable differences between species of these 2 groups are: members of the "*Anisotarsus*" group have the dorsal membranous area of the median lobe elongate, reaching the basal bulb, and have the hindtarsus with the first segment shorter than II + III; members of the "*Diaphoromerus*" group have the length of the dorsal membranous area of the median lobe, and the relative lengths of the first 3 segments of the hindtarsus varying from one species to the next.

The presence of such similar species groups in the New World and the Australian Region is best explained by assuming that members of the South American temperate adapted stock crossed during the Tertiary into the Australian Region by using Antarctica and possibly several intervening islands as stepping stones. (Antarctica and Australia did not become appreciably separated until probably some time in the Tertiary (Dietz and Holden, 1970; Smith and Hallam, 1970). An alternative, but less probable, explanation for the presence of such similar groups in the New World and Australian Region is that these 2 groups are simply polyphyletic assemblages of plesiomorphic forms which arose separately in the New World and Australian Region and did not differentiate as did the other forms of Anisodactylina.

The second or Anisodactyloid main branch consists of those forms in which the mentum and submentum are either fused laterally and separate medially or completely fused. This branch is absent from the Australian region, suggesting that it did not originate there, and also is absent from South America. It probably arose in Africa or somewhere on the combined Eurasia-North America landmass after Africa had become well separated from South America. The Anisodactyloid groups while often each possessing apomorphic character states do not share synapomorphies among themselves; this suggests a moderately long period of evolution with extinction of many groups taking place during such evolution. Therefore, the Anisodactyloids probably originated in late Cretaceous or early Tertiary.

The Anisodactyloids (Fig. 241) arose from a lineage of the presumably once widespread Notiobioid main branch and then displaced this more plesiomorphic group from most areas. In Fig. 240 the Anisodactyloids are shown to arise after the genus *Scybalicus*, a remnant of the once more widespread Notiobioid main branch. A dotted line is used to emphasize that the exact time of origin of the Anisodactyloids is not clear and that *Scybalicus* is *not* their sister group.

Chorologies of extant groups of the Anisodactyloids suggest, but do not prove, an origin in temperate southern Africa.

Tropical Africa contains the genus *Progonochaetus* most of whose species have the mentum and submentum fused laterally but still separated medially. This genus thus contains species in which the state of the mentum and submentum is intermediate between the plesiomorphic state of completely separate and the apomorphic state of being completely fused. Therefore, it seems probable that the Anisodactyloid main branch passed through tropical Africa in an early stage of its evolution.

The Anisodactyloid main branch is today absent from the African tropics except for: *Progonochaetus*; the primarily Oriental genus *Pseudognathaphanus* which has 2 species on Madagascar; and the monotypic genus *Phanagnathus* found in the Zaire Republic (former Belgian Congo). The latter 2 genera contain species with mentum and submentum completely fused. The Madagascar species of *Pseudognathaphanus* are little differentiated from those of the Orient and probably dispersed from the Orient to Madagascar during the Pleistocene when for long periods much of the Sahara received plentiful rain (Moreau, 1966). Alternatively, the genus *Pseudognathaphanus* may have originated in tropical Africa, dispersed from there to the Orient and to Madagascar, and then became extinct in Africa. The genus *Phanagnathus* neither seems closely related by synapomorphy to other taxa of the Anisodactyloid main branch nor does it seem itself to possess many apomorphic characters. Therefore, this genus most likely arose early in the evolution of the Anisodactyloids and then became both geographically and phylogenetically isolated with extinction of its closest relatives.

Except for *Rhyssopus*, the species of the Anisodactyloid genera of tropical Africa, Madagascar, and tropical Asia all possess a plesiomorphic type of ligula which is slender and not or at most only moderately expanded laterally at the apex. With the exception of *Xestonotus* and the subgenus *Amphasia*, the Anisodactyloid groups of temperate Eurasia and temperate North America have the apomorphic form of ligula with apex moderately to strongly expanded laterally. Thus, the African and Oriental groups of Anisodactyloids are relatively more plesiomorphic than the temperate North American and Eurasian ones.

In late Cretaceous, Africa was situated further south than at present (Dietz and Holden, 1970). It is thus likely that northern Africa was tropical while a large portion of southern Africa was temperate. The most probable pattern of evolution of the Anisodactyloids was one of evolution in temperate southern Africa with an early dispersal northwards through the tropics to the Orient and temperate Eurasia. The evolving Anisodactyloids presumably displaced the previous Notiobioid fauna from Africa and Eurasia (except for the genus *Scybalicus*) and displaced the Notiobioid fauna of North America (except for the genus *Notiobia*).

The ancestral Anisodactyloids then arose in temperate southern Africa and early in their evolution acquired the feature of mentum and submentum fused laterally but free medially. The ancestral Anisodactyloids twice (Figs. 250, 251) invaded more northern tropical portions of Africa, to give rise to 2 different branches. Ultimately, the ancestral stock in temperate southern Africa became extinct, quite possibly due to a contraction of southern temperate areas as Africa moved northward.

The first of the tropical adapted branches (Fig. 250) retained a partially fused mentum and submentum but acquired the apomorphic features shown in Fig. 241. This branch eventually gave rise to the subgenera *Progonochaetus* and *Eudichirus* of the mainly African genus *Progonochaetus*. One species of the subgenus *Progonochaetus*, *laevistriatus*, is present in tropical India and Burma. It may have dispersed to the Oriental Region relatively recently, such as during climatic changes of the Pleistocene; or *Progonochaetus* may once have been widespread in the Oriental Region and only recently receded from this area. The Oriental Region has not been well collected for Carabidae, and additional species of *Progonochaetus* may be present there.

The second movement of ancestral Anisodactyloid stock into tropical Africa produced the second branch with the more apomorphic feature of mentum and submentum completely fused. Some members of the second branch moved (Fig. 251) through the tropics of Africa into the tropics of the Oriental Region and radiated there. Others migrated (Fig. 251) into temperate portions of North America-Eurasia and underwent considerable radia-

tion there. Thus, the second branch was split into tropical adapted forms inhabiting the tropics of Africa and the Orient, and into temperate adapted forms inhabiting temperate regions of Eurasia. The tropical adapted forms (except for *Rhysopus*) retained the plesiomorphic slender form of ligula while the temperate adapted ones (except for *Xestonotus*) evolved an apomorphic form of ligula with a broader apex; the slender ligula of *Amphasia* is secondarily derived from the apomorphic ligula.

As it moved through Africa and into the tropics of the Orient, the second tropical adapted branch possibly gave rise to the genus *Pseudognathaphanus*. This genus today is represented in the Ethiopian Region only by 2 endemic Madagascar species which are little different from Oriental species. Thus, *Pseudognathaphanus* may have evolved in the Oriental Region and later during Pleistocene climatic changes dispersed from there to Madagascar via Africa.

The relatively apomorphic Oriental sister stock of *Pseudognathaphanus* split into the *Chydaeus* and *Rhysopus* lineages in the Oriental Region. The former lineage gave rise to the moderately apomorphic genus *Chydaeus*. The *Rhysopus* lineage possessed numerous apomorphic character states (Fig. 241) and subsequently divided to produce the genera *Harpalomimetes* and *Rhysopus*.

In the phylogeny and dispersal of North Temperate Anisodactyloids, I postulate that ancestors of all North American taxa except *Dicheirus* crossed (Fig. 252) from Eurasia into North America via the broad connection existing between western Europe and North America until some time in late Cretaceous (Dietz and Holden, 1971). Dispersal of Eurasian animals into North America is traditionally explained by invoking the Tertiary Bering Land Bridge. However, most North American Anisodactyloid groups are concentrated in the east and form a subtraction pattern towards the west. And the Anisodactyloid fauna of Eurasia is concentrated in Europe and the Mediterranean area and forms a similar subtraction pattern towards Siberia. Thus, the distribution patterns of North Temperate Anisodactyloids in most instances support dispersal into North America via the connection with Europe.

Objection may be made that if Anisodactyloids reached North America in late Cretaceous, they should have reached the present Mexican highlands before the Pliocene development of an arid zone barrier in southern Texas and northeastern Mexico (Martin and Harrell, 1957). However, there is no reason why immigrants reaching North America must immediately (if ever) have dispersed southward. They must first adapt to the new habitats presented in North America. Further, the subgenus *Anadaptus*, which I postulate arose soon after arrival of its ancestral stock in North America, does contain a species in the Mexican highlands.

The possibility that all North American Anisodactyloids arrived via the Bering Land Bridge can not be disproved. It may be that increasing aridity and cold developing in late Tertiary in Siberia and western North America destroyed the faunas of these areas. However, for all groups except *Dicheirus* I prefer the postulated crossing from western Europe to North America since distribution patterns do support this dispersal route but do not support dispersal across the Bering Land Bridge.

The temperate adapted substock in Eurasia probably early evolved the apomorphic feature of ligula apex expanded laterally. The genus *Xestonotus* is characterized by the apomorphic feature of a strongly asymmetrical median lobe but also has a ligula apex which is not expanded laterally. This genus may have evolved before the temperate adapted substock acquired the apomorphic feature of ligula apex expanded laterally, or if afterward, its narrow ligula represents a secondary reversion. Although such reversion has occurred in the subgenus *Amphasia*, it seems best to provisionally treat *Xestonotus* as having evolved just before the temperate adapted substock acquired a laterally expanded ligula apex. Since *Xestonotus* is restricted to eastern North America, its ancestor probably evolved in Eurasia,

crossed over into eastern North America via the Europe-eastern North America connection (Fig. 252), and then became extinct in Eurasia.

The temperate adapted stock in Eurasia early split into a substock retaining the plesiomorphic condition of body generally glabrous and into a substock with body generally pubescent. The possibility of the latter substock being diphyletic due to convergence is treated later in this discussion. Part of the generally glabrous bodied substock then crossed over into North America via the Europe-eastern North America connection (Fig. 252) and radiated there. The substock remaining in Eurasia in turn underwent radiation in that region.

The portion of the substock in Eurasia first divided into the *Gynandrotarsus* and *Anisodactylus* lineages. The *Gynandrotarsus* lineage was distributed across western Eurasia and eastern North America before the final rupture of the two continents in the Cretaceous. The separation of the continents divided the lineage into the *Gynandrotarsus* and *Pseudodichirus* sublineages restricted respectively to North America and Eurasia. The remaining portion of the generally glabrous bodied substock split into the *Anisodactylus* and the *Hexatrichus* branches. The first branch retained unmodified male foretibia and gave rise to the subgenera *Anisodactylus* and *Pseudanisodactylus*. The ancestor of the *Hexatrichus* branch possessed the apomorphic feature of male foretibia moderately emarginate along inner proximal margin. The branch subsequently split into: the subgenus *Hexatrichus* with male foretibia having strongly emarginate inner proximal margin; and the subgenus *Pseudhexatrichus*, with ancestral form (that is only moderately emarginate) of male foretibia.

Early in its history, the generally glabrous bodied substock in North America produced the subgenus *Anadaptus* characterized by: the apomorphic character states of short, stout hindtarsus and median lobe bearing "button"-like apical disc; and the plesiomorphic character state of stylus with glabrous basal segment. The *Aplocentrus* sister branch to the subgenus *Anadaptus* had the apomorphic character state of setae present on basal segment of stylus and the plesiomorphic character state of hindtarsus not short and stout. The *Aplocentrus* branch divided into the subgenus *Spongopus* whose sole species lacks any dorsal metallic tinge, and the subgenera *Aplocentrus* and *Pseudaplocentrus* whose ancestor had a slight metallic tinge on the dorsum.

The genus *Geopinus* most probably arose from some now extinct lineage around the time that *Anadaptus* and the *Aplocentrus* branch were produced. This genus contains only the species *incrassatus* which is highly adapted to a fossorial mode of life. This species has very short, stout hindtarsus and in general habitus resembles *Anadaptus discoideus*. However, *incrassatus* has setae on the basal segment of the stylus and does not have an apical disc on the median lobe. In addition, it has highly modified fossorial fore- and midtibia and an antennal sulcus. The most probable ancestry of *Geopinus* is indicated with a dotted line in Fig. 241.

The Eurasian substock with a generally pubescent body is composed of 2 distinct lineages united only by the apomorphic character state of body generally pubescent. The length, thickness, and density of body pubescence is considerably varied among the species of each lineage. And occasional species of *Anisodactylus*, such as *consobrinus*, have independently evolved considerable body pubescence. There is thus a possibility that the substock with a generally pubescent body is diphyletic due to convergence. However, no extant taxa in either lineage of this substock have close affinities to taxa in the generally glabrous bodied substock, and I therefore assume that the pubescent bodied substock is monophyletic.

The pubescent bodied substock early split into the genus *Amphasia* and the *Dicheirus* lineage. The ancestor of *Amphasia* was characterized by the apomorphic character state of stylus moderately dorso-ventrally flattened, apical segment with small teeth along lateral margin and small spines arising between these teeth. Since the 2 extant species of this genus

are restricted to eastern North America, the ancestor of the genus probably crossed into North America before eastern connections with Eurasia were severed in late Cretaceous. The genus ultimately split into the subgenera *Pseudamphasia* and *Amphasia*. The former subgenus has a moderately modified stylus such as in the ancestor of the lineage while the subgenus *Amphasia* has a more apomorphic type of stylus. In addition, the ligula apex of *Amphasia* has secondarily reverted to the condition of not expanded laterally.

The *Dicheirus* lineage probably evolved in Eurasia and at one time extended as far east as the present Bering Strait area. The ancestral stock of this lineage had the apomorphic character states of: frontal fovea obscured by punctures; mental tooth present; and small setae present on distal margin of basal segment of stylus. The genus *Dicheirus* is restricted to western North America, its ancestor having crossed over the Bering Land Bridge in early or middle Tertiary. The ancestor of *Dicheirus* was characterized by the apomorphic conditions of: foretibial apical spur trifid; and pronotal apical bead absent. The sister sublineage to *Dicheirus* retained the plesiomorphic condition of pronotal apical bead present at least laterally, possibly also the plesiomorphic condition of foretibial apical spur lanceolate, and acquired the apomorphic condition of dorsum brightly tri-colored. This sister sublineage subsequently split into the genera *Gynandromorphus* and *Diachromus*. The former is characterized by the apomorphic feature of a trifid foretibial apical spur while the latter has the apomorphic conditions of 2 pronotal lateral setae and the intermediate character state of foretibial apical spur swollen laterally.

#### Evolutionary Trends and Convergences within Anisodactylina.

The most notable evolutionary feature of the postulated phylogeny is the trend from mentum and submentum separated by a complete transverse suture to mentum and submentum completely fused. Twelve supra-specific taxa have the mentum and submentum separated by a complete transverse suture, 2 have the mentum and submentum usually fused laterally but separated medially by a transverse suture, and 23 have the mentum and submentum completely fused. There are 2 instances within the Notiobioid main branch of convergence towards the condition of mentum and submentum fused: mentum and submentum completely fused in all species of *Anisostichus*; suture between mentum and submentum narrow and apparently in process of being lost in few species of "*Paradiatypus*" group of subgenus *Diatypus*. A study of the possible functional advantage of a fused mentum and submentum would be worthwhile. Possibly such fusion strengthens the mouth area and enables beetles to feed on hardened material such as seeds.

Presence or absence of a mental tooth may be somewhat correlated with the state of the mentum and submentum. Most Notiobioids have a moderate sized mental tooth, clearly plesiomorphic within this main branch. Apparently the ancestor of the Anisodactylids lacked a mental tooth for most Anisodactylids do not have one or have only a slight swelling on the middle margin of the mentum. The mental tooth within the Anisodactylid main branch is therefore apomorphic if present.

Several groups have evolved adaptations for burrowing. The most striking such adaptations are found in the highly fossorial *Geopinus incrassatus*. This species possesses the following features presumed to be adaptations for burrowing: a broad antennal sulcus in front of each eye for receiving antenna in repose (to protect antenna during burrowing); an apically enlarged foretibia (to strengthen foretibia and make it more effective in dirt removal); a foretibia bearing large excavate dilation externally at apex (to scoop away soil and protect tarsus); spatulate hindtibial apical spurs (useful in burrowing); a short hind-tarsus (to decrease damage during digging); a narrow pronotum (to enable beetle to insert fore part of body into narrow openings prior to enlarging them); and a mandible with

deeply striate apex (resulting roughness of apex possibly of advantage in moving dirt during burrowing).

Other less fossorial Anisodactylines possess features which may also be adaptations for burrowing. Species of the genus *Dicheirus* occur on the soil surface under debris on the ground and also in worm holes and shallow burrows just beneath such debris. The body of *Dicheirus* is relatively slender, which should help in moving through burrows, and the trifold foretibial apical spur probably is advantageous in burrowing. In addition, females of *obtusius* have spatulate hindtibial apical spurs which presumably also are advantageous in burrowing.

Species of the subgenus *Anadaptus* also may be somewhat fossorial; I have taken several specimens referable probably either to *porosus* or *alternans* from shallow burrows beneath litter on the ground. Except for the somewhat stouter *discoideus*, species of *Anadaptus* are semicylindrical, which suggests adaptation for movement in burrows; all species have short hindtarsi as in *Geopinus incrassatus*; and the foretibial apical spur is thickened and subtrifold in some specimens.

Species of the subgenus *Gynandrotarsus* are semifossorial. I have taken specimens of *rusticus*, *ovularis*, *harpaloides*, *dulcicollis*, and *anthracinus* in shallow tunnels beneath debris on the ground and have taken *ovularis* and *rusticus* by digging up clumps of grass. However, the only noticeable morphological adaptation in species of *Gynandrotarsus* for burrowing is the strongly trifold foretibial apical spur.

The styli of *Pseudamphasia* and *Amphasia* form an interesting morphocline. The plesiomorphic type of stylus (Fig. 237) within the subtribe is not dorso-ventrally flattened, not laterally expanded, lacks serrations, and has 2 closely situated setae on the distal mesal margin of the apical segment. The stylus of *Pseudamphasia* (Fig. 233) is moderately dorso-ventrally flattened, moderately expanded laterally, and has an apical segment with a finely serrate lateral margin bearing very small spines between the serrations. The stylus of *Amphasia* (Fig. 234) is even more apomorphic and is strongly dorso-ventrally flattened, strongly expanded laterally, and has an apical segment with a prominently serrate lateral margin bearing stout spines between the serrations.

The valvifers within 5 subgenera of *Anisodactylus* form a morphocline from a triangular ancestral type (Figs. 217, 218, 219) with distal setae, to a subtriangular type which lacks distal setae, and bears a distal concave area (Fig. 130). The ancestral type is found in *Anisodactylus* and *Pseudhexatrachus*. An intermediate subtriangular type with distal setae (Fig. 222) is found in *Hexatrachus*. In *Pseudodichirus* (Fig. 220) the valvifer in addition to being subtriangular is further modified by loss of all distal setae. Lastly, in *Gynandrotarsus* the valvifer not only is subtriangular and lacks distal setae but has acquired a distal concave area (Fig. 130).

Table 3 (p. 435) summarizes instances of convergence noted among supra-specific taxa of Anisodactylina. Two of these instances are further discussed here. In the past, several polyphyletic supra-specific groups have been defined on the basis of their species possessing a trifold foretibial apical spur. Examination of other characters has convinced me that the trifold type of spur has arisen by convergence within 4 monophyletic supra-specific groups: (1) in 3 species of the subgenus *Anisodactylus*; (2) in the single species of the genus *Rhysopus*; (3) in all species of the subgenus *Hexatrachus*; and (4) in the common ancestor of the sister subgenera *Pseudodichirus* and *Gynandrotarsus*. The species of the genera *Gynandromorphus* and *Dicheirus* also possess a trifold foretibial apical spur, due to convergence or not. If not, then the spur of the sole species of *Diachromus* (sister genus to *Gynandromorphus*) has secondarily reverted to the non trifold state. Trifold foretibial apical spurs may also be evolving in other groups such as *Anadaptus*, *Gnathaphanus*, and *Scybalicus* in which few or all members of some species have the spur slightly angulate on each side or even some-

what subtrifid. The evolutionary reason for convergence in trifid spurs is probably increased efficiency in burrowing.

The shape of the ligula also demonstrates interesting convergences. The plesiomorphic type of ligula is slender and with apex not or only very slightly laterally expanded. An apomorphic type of ligula in which the apex is moderately to strongly expanded laterally has independently arisen in: (1) some specimens of *Notiobia* (*Anisotarsus*) *tucumana*; (2) the "*Paradiatypus*" species group of the subgenus *Diatypus*; (3) the genus *Criniventer*; (4) the genus *Rhyssopus*; and in all temperate adapted Anisodactyloids except for the genus *Xestonotus*. In addition, the ligula of *Amphasia* has secondarily reverted back to the narrow form without an expanded apex.

### Phylogeny of the New World Species of the Subgenus *Anisotarsus*.

Table 4 (p. 436) summarizes the plesiomorphic and apomorphic character states employed in reconstructing the phylogeny illustrated in Fig. 242. The ancestor of *Anisotarsus*, which arose in temperate areas of southern South America, possessed the plesiomorphic character states listed in Table 4 (p. 436) and in addition had: body and appendages rufopiceous to black, dorsum lacking metallic color or tinges; microsculpture of isodiametric mesh; and dorsal membranous area of median lobe extended to basal bulb.

In the early or middle Tertiary a species of *Anisotarsus* dispersed to North America by crossing water gaps between various islands in the present Central American and Caribbean areas. This species early gave rise to the *cyanippa* and *terminata* branches. The first branch retained the ancestral feature of wide gena while the second one acquired apomorphic narrow gena. The *cyanippa* branch subsequently split into the *cyanippa* and *brevicollis* lineages. The former lineage retained the plesiomorphic feature of only 2 ambulatory setae on the sixth abdominal sternum of males but possessed the apomorphic features of pronotal posterior angle moderately to strongly rounded and hind wing vestigial or dimorphic. The lineage ultimately produced the Mexican species *hilariola* and *cyanippa*. I have seen 1 male of *hilariola* with 4 ambulatory setae on the sixth abdominal sternum; this may be an aberrant specimen, or the number of such setae may vary in males of *hilariola*, or a relationship with the *brevicollis* lineage may be indicated. The *brevicollis* lineage retained the ancestral type of pronotal posterior angle and hind wing but possessed the apomorphic feature of 4 ambulatory setae on the sixth abdominal sternum of males. The primarily Mexican species *brevicollis* is the only extant representative of this lineage.

A major weakness in linking the *brevicollis* and *cyanippa* lineages is the apparent lack of synapomorphies between them. However, the *brevicollis* lineage certainly does not seem to belong to the *terminata* branch, and chorology suggests that its closest extant relative is the *cyanippa* lineage. Extinctions in both the *brevicollis* and *cyanippa* lineages as well as of any possible intermediate lineages may explain the lack of synapomorphies.

Due apparently to a complex history of radiation and to subsequent extinctions of many species, only the *nitidipennis* lineage within the *terminata* branch can be defined by clearly apomorphic features. The *nitidipennis* lineage is composed of the species *nitidipennis* and *schlingeri* characterized by the apomorphic states of eye usually relatively small and pronotal side straight or sinuate basally. The 2 species are geographically disjunct and appear to be sister species.

The 3 species *flebilis*, *purpurascens*, and *terminata* are not united by any clearly apomorphic characters but probably form a single lineage, the *terminata* lineage, for the following reasons. The species *flebilis* and *purpurascens* were formerly considered to be subspecies of a single common species, because of their strikingly similar general habitus and because their pronotal sides were moderately convergent basally. Indeed, their general habitus is so

similar that it is often difficult to separate teneral females of *purpurascens* from females of *flebilis*. The legs and first antennal segment of these 2 species are always testaceous to rufous in color. Such coloration occurs in several other species of *Anisotarsus*, but the more common and possibly, therefore, more plesiomorphic condition is that of darker legs and antenna. The species *flebilis* is known only from Guadalupe Island, southern Baja California, and the Mazatlan region of Mexico, and it may represent an isolated relict species of a formerly widespread ancestral stock.

The species *purpurascens* shares relationships to *terminata*, but these relationships are complicated by the wide character variability found in *terminata*. The species *purpurascens* has a general habitus very similar to that of some specimens of *terminata* which have the pronotal sides moderately convergent basally, pronotal lateral depression obsolete, and elytron lacking a greenish tinge. These character states occur in occasional specimens of the Texas, Florida, and Mexico morphs of *terminata*, and some specimens of the 2 species appear so similar in external features that they are very difficult to separate. The median lobe of *purpurascens* is stout in form and very similar to that found in the northern morph of *terminata*. The median lobes of Texas, Florida, and Mexico morphs of *terminata*, however, are typically more slender in form than that of the northern morph or of *purpurascens*. And specimens of the northern morph differ from *purpurascens* in having a wide prominent pronotal lateral depression. Also, *terminata* always has the same light colored legs and first antennal segment as do *purpurascens* and *flebilis*. It is reasonable to conclude that these 3 species came from the same ancestral stock.

The species *virescens*, *maculicornis* and *picea* are evidently derived from the same ancestral stock which gave rise to the *terminata* and *nitidipennis* lineages. However, it would appear that these 3 species are the survivors of an early species radiation or radiations as they do not show close relationships to each other or to either the *nitidipennis* or *terminata* lineages. The species *picea* is somewhat isolated from *virescens*, *maculicornis* and the *terminata* lineage by the combination of 4 setae on the sixth abdominal sternum in males and pronotal microsculpture obsolete medially. Since both *picea* and *schlingeri* have 4 setae in the male, *picea* may possibly be the sole survivor of a once larger lineage containing species linking the *terminata* and *nitidipennis* lineages. The species *virescens* and *maculicornis* do not show close relationships to *picea* or to the *terminata* or *nitidipennis* lineages. In the absence of further data, it is impossible to state more than they probably were derived from the same general stock as these forms due to their also sharing the plesiomorphic condition of wide gena.

The *Anisotarsus* stock which remained in South America early acquired the apomorphic features of distal setae present on elytral intervals III, V, and VII and internal sac of the median lobe lacking a large spine. It then split into the *tucumana* and *mexicana* branches.

The *tucumana* branch was characterized by the apomorphic features of pronotal posterior angle moderately to strongly rounded and sixth abdominal sternum of males with 4 ambulatory setae. It soon divided into 2 lineages: the *cupripennis* lineage whose members possessed the plesiomorphic condition of a prominent mental tooth; and the *tucumana* lineage whose members possessed the apomorphic condition of mental tooth absent or vestigial. The *cupripennis* lineage is composed of 8 named forms and needs further study before the exact relationships of its forms can be elucidated.

The *tucumana* lineage contains 2 named South American species, *tucumana* and *bradytoides*, and 1 unnamed species which in this discussion and in Fig. 242 is termed species "A". Additional study of South American *Anisotarsus* may reveal more undescribed species and change some of my conclusions presented below concerning the evolutionary history of this lineage.



The *tucumana* lineage evidently gave rise early in its history to a species or group of species possessing only a vestigial mental tooth. This ancestral species or species group in turn produced the species *bradytoides* possessing a vestigial mental tooth and the plesiomorphic conditions for the ligula, abdominal pubescence, and median lobe. Also this ancestral species or species group gave rise to a species completely lacking a mental tooth and possibly possessing some additional setae on abdominal sterna IV and V. This species then ultimately gave rise to *tucumana* and to species A. The latter species in addition to lacking a mental tooth possesses the apomorphic condition of having a few fine short additional setae on the fourth abdominal sternum. The species *tucumana* possesses the additional apomorphic features of: ligula with apex moderately to prominently widened as in *Anisodactylus*; abdominal sternum IV and V bearing extra setae (more numerous in male); posterior margin of hind femur with 10 to 12 setae; and median lobe highly asymmetrical. Also the internal sac of the median lobe of *tucumana* apparently regained a large prominent spine, unless some past ancestors of the *tucumana* lineage retained this feature, or unless the *tucumana* lineage is polyphyletic. The possession of these strikingly apomorphic character states suggests that *tucumana* may be the end result of a serial evolution of several species from the original ancestor of species A.

The *mexicana* branch possessed the apomorphic feature of pronotal lateral bead very prominent, and the additional feature of females having eighth abdominal tergum with obtusely angulate apex. During early Pliocene a member migrated to North America via the newly established Central American connection between North and South America. The member migrating to North America gave rise there to the *mexicana* lineage while the stock remaining in South America produced the *chalcites* lineage.

The *chalcites* lineage acquired the apomorphic features of metallic tinges on dorsum and 4 ambulatory setae on sixth abdominal sternum of males, and retained the postulated ancestral type of female eighth abdominal tergum. It subsequently split to produce the named forms *chalcites* and *amethystina*.

The ancestor of the *mexicana* lineage retained the ancestral features of non-metallic tinged dorsum and male sixth abdominal sternum with only 2 ambulatory setae. The lineage produced the species *lamprota*, which evolved metallic tinges but retained the ancestral type of female eighth abdominal tergum, and the species *mexicana* which retained a non-metallic dorsum but acquired the apomorphic features of female eighth abdominal tergum rounded at apex and antennal segments short.

The apomorphic character state of 4 ambulatory setae on male sixth abdominal sternum has arisen 5 times by convergence, and the apomorphic character state of rounded pronotal posterior angle did so twice. These convergences are not surprising since the characters these states represent are not especially constant within Anisodactylina. The instances of convergence in number of male ambulatory setae could be reduced to 4 by connecting the *brevicollis* lineage to the *tucumana* branch. However, this would require: an additional invasion of North America; secondary loss in the *brevicollis* lineage of distal setae on elytral intervals III, V, and VII; and secondary regaining in the *brevicollis* lineage of a large spine on the internal sac of the median lobe. Similarly, and over similar objections, convergence in rounded pronotal posterior angles could be eliminated by connecting the *cyanippa* lineage to the *tucumana* branch.

Except for the *mexicana* lineage, the North American and South American species do not show any close phylogenetic relationships. The reasons for this general lack of close phylogenetic relationships are discussed in the section on historical zoogeography.

### Remarks on the Phylogeny of the Species of the Subgenus *Notiobia*.

In this paper I am revising only 10 of the 24 named species of this subgenus. Several of these revised species are recorded from Central or South America, and additional collecting will undoubtedly result in additional ones being recorded from these regions. In several instances I have noted that the closest relatives of Mexican species appear to be found in Central or South America, and I have seen many specimens from Central and South America which appear to be new species. I feel that it would be unproductive to attempt constructing a phylogeny of *Notiobia* (s. str.) until the Central and South American forms are better known.

### Phylogeny of the Species of the Subgenus *Gynandrotarsus*.

Table 5 (p. 438) summarizes the plesiomorphic and apomorphic character states employed in the reconstructed phylogeny presented in Fig. 243. The ancestor of *Gynandrotarsus* possessed the plesiomorphic character states listed in Table 5 (p. 438) and in addition had: body with microsculpture of isodiametric mesh; 4 ambulatory setae on male abdominal sternum VI; and no large armature on internal sac of median lobe.

The ancestor of *Gynandrotarsus* most likely arrived in eastern North America during late Cretaceous or early Paleocene via the connection with the European part of Eurasia. The ancestor then produced the *harpaloides* and *merula* stocks. It seems most likely that the common ancestor of these stocks possessed the character state of a raised transverse ridge behind the clypeal apex. Such a transverse ridge is present in all species of the *merula* stock and in the species *opaculus* of the *harpaloides* group. It is more probable that this structure was lost in the other species of the *harpaloides* stock than that it evolved independently in *opaculus*. It should be mentioned here that *opaculus* is not intermediate between the *harpaloides* and *merula* stocks simply because females of *opaculus* have the first segment of the foretarsus strongly laterally expanded and most specimens of both sexes have a slight dorsal greenish tinge. In my opinion, the presence of a raised transverse ridge behind the clypeal apex is a plesiomorphic character state within the subgenus *Gynandrotarsus* while it is an apomorphic character state when comparing the subgenera of *Anisodactylus*. Conversely, the absence of such a ridge, which is plesiomorphic in the genus *Anisodactylus*, is apomorphic within *Gynandrotarsus*.

The *harpaloides* stock was characterized by the apomorphic character state of first foretarsal segment slightly to moderately expanded laterally in females, and by the plesiomorphic character states of: clypeo-ocular prolongation; raised transverse ridge behind clypeal apex; and apical disc on median lobe. This group subsequently split into the *harpaloides* and *texanus* lineages. The first lineage possessed the apomorphic character states of: median lobe lacking apical disc; greenish tinge present on dorsum; and first segment of female foretarsus strongly expanded laterally. The *texanus* lineage in turn retained the ancestral states of these characters.

The *harpaloides* lineage ultimately gave rise to the species *opaculus* and *harpaloides*. The species *opaculus* has prominent dorsal microsculpture whereas *harpaloides* and the two extant species of the *texanus* lineage have reduced dorsal microsculpture. Therefore, there may have been a series of ancestral species giving rise ultimately to *opaculus*.

The *texanus* lineage finally produced the species *texanus* and *dulcicollis*. As these two species are not related by any special synapomorphies, and as they are not extremely similar phenetically, they may represent the sole survivors of a larger assemblage of species derived from the *texanus* lineage.

The *merula* stock was characterized by the apomorphic features of clypeo-ocular prolongation absent and pronotum moderately widened basally.

Evidently, at an early stage in its evolution the *merula* stock produced the now monotypic *haplomus* branch characterized by the apomorphic character states of: pronotal lateral bead obsolescent anteriorly, fine elsewhere; microsculpture of frons of isodiametric punctures; elytral subapical sinuation prominent; and pronotum prominently widened basally. The latter feature is also possessed by the species *merula*, but I believe this is due to convergence.

The remaining 5 species of the *merula* stock form the *merula* branch which is defined only on the basis of symplesiomorphy. Therefore, the following postulated sequence of evolution is based on chorology and relative degree of apomorphy shown by each species. The *merula* branch produced the now widespread monotypic *rusticus* lineage, characterized by the apomorphic feature of median lobe lacking apical disc. The complimentary *merula* lineage retained the plesiomorphic feature of median lobe with apical disc present and split into the *ovularis* and *merula* sublineages. The *merula* sublineage possessed the apomorphic feature of humeral tooth present while the *ovularis* sublineage retained the plesiomorphic state of tooth absent. The *merula* sublineage includes *merula* and *anthracinus*, which have identical median lobes, show spatial vicariance (Figs. 160, 161), and are recently evolved sister species. The *ovularis* sublineage gave rise to *ovularis* and *darlingtoni*, which are not united by clearly apomorphic character states but have very similar general habitus.

## ZOOGEOGRAPHY

### Introduction

This section discusses the zoogeography of supra-specific taxa of Anisodactylina and of species of *Anisotarsus*, *Notiobia* (*s. str.*), and *Gynandrotarsus*. Both contemporary and historical zoogeography are treated for *Anisotarsus* and *Gynandrotarsus*. Information on ecology of species of the other 35 groups is limited as is information on past climates, flora, and fauna of the areas they inhabit. It was necessary to use all available information on historical zoogeography of the supra-specific taxa in order to elucidate their phylogenetic relationships. Consequently, this information has been incorporated into the section on phylogeny of the supra-specific taxa. And the zoogeography of the species of *Notiobia* (*s. str.*) is only very briefly treated for reasons outlined in the subsection on them.

### Contemporary Zoogeography of the Subtribe Anisodactylina.

The 6 major faunal regions (Nearctic, Neotropical, Palearctic, Ethiopian, Oriental, and Australian) were originally proposed by Sclater (1858), on the basis of bird distributions, confirmed by Wallace (1876) for vertebrates and some invertebrates, and reconfirmed and further discussed by Darlington (1957) for vertebrate distribution. Darlington (1957) stated that Madagascar was traditionally placed in the Ethiopian region, but that he preferred to treat it separately. Heilprin (1887) combined the northern regions, the Palearctic and Nearctic, into a Holarctic Region on the basis of vertebrates shared between the two areas. Kuschel (1963) discussed arguments for treating southern South America, southern Africa, Antarctica, and the Australian area as a distinct "Austral Region". He pointed out (p. 448) that the distribution of weevils "definitely points to an Austral Region; but I would also say that such a big step would need to be based on many groups."

I agree with Kuschel that such a "big step" should be based on many groups. I also believe that invertebrates in general, and insects in particular, have been neglected when zoologists attempt to divide the world into major faunal regions. Workers revising previously little understood groups should endeavor to analyze the regional divisions suggested by the distribution of included taxa. This analysis should be done so that future zoogeographers

can consider possible changes in the major faunal regions as suggested by distributional data from many different groups of invertebrates. I endeavor below to analyze the correlation of distribution of groups of Anisodactylina with the 6 major faunal regions as defined by Wallace (1876) and as modified by Heilprin (1887), Darlington (1957), and Kuschel (1963).

The bottom of Table 6 (p. 440) gives the distribution of groups in terms of the 6 faunal areas as defined by Wallace (1876); genera and subgenera are treated as equivalents and termed "groups".

Data from Table 6 (p. 440) indicate that the Nearctic and Palearctic Regions should be retained as separate major faunal regions. Ten or 83 percent of the 12 groups found in the Nearctic Region are endemic while 6 or 67 percent of the groups found in the Palearctic are endemic. The 2 regions share only 1 group, the subgenus *Anisodactylus*.

The Palearctic Region, consisting basically of temperate Eurasia, contains a single center of concentration embracing Europe (especially the southern part) and the lands surrounding the Mediterranean. Six of the 9 groups present in the Palearctic Region are endemic to this center of concentration: *Scybalicus*, *Pseudhexatrachus*, *Hexatrachus*, *Pseudodichirus*, *Gynandromorphus*, and *Diachromus*. An additional group, the subgenus *Anisodactylus*, has some of its species occurring in this center of concentration.

The eastern part of temperate Eurasia (Siberia, north and central China, Japan, and Korea) is relatively depauperate in number of groups. Four groups, *Chydaeus*, *Harpalomimetes*, *Anisodactylus*, and *Pseudanisodactylus* occur there. The only group which appears endemic to eastern Eurasia is *Pseudanisodactylus* which apparently is restricted to Japan, Korea, and China. *Chydaeus* on mainland Eurasia enters only the southern part of the Palearctic Region in Tibet and central China and offshore extends only to Japan. The 2 species of *Harpalomimetes* are mostly concentrated in the Oriental Region, and only one of them extends as far north as Japan and thus into the Palearctic Region. The species of *Anisodactylus* in Eurasia generally have wide distributions ranging from temperate Europe to Japan.

The Oriental Region consists essentially of tropical southern Eurasia together with the Philippines and the Indo-Australian Archipelago. Darlington (1957) pointed out the lack of sharp boundaries for this region. The western boundary in India is uncertain, and the dry country of northwestern India has an impoverished vertebrate fauna with transitions occurring from east to west and from north to south. In the northeast the Himalaya forms a natural boundary, but this boundary occurs several degrees north of the tropics. Further east the boundary of the Oriental Region becomes more difficult to fix, and there is a broad, complex transition between the Palearctic and Oriental Regions. And the Oriental fauna forms a broad complex transition with the Australian fauna beyond Java and Borneo.

The distributions of groups of Anisodactylina support these views of Darlington, and the lack of sharp natural boundaries for this region is reflected by the low rate of endemism here. Of the 9 groups represented, only *Rhyssopus* is endemic. The genus *Chydaeus* centers in southern China, northern India, and Sikkim of the Oriental Region but also in Tibet which is north of the Himalayas and thus in the Palearctic Region. The genus extends to central China, and Japan, and eastward on mountain tops along the Indo-Australian Archipelago to New Guinea. *Harpalomimetes* is centered in the Oriental Region but does occur in Japan and goes as far towards Australia as the Philippines. *Hypharpax* is an Australian group which has 3 species reaching as far into the Oriental Region as Java. The genus *Gnathaphanus* is another Australian group, but species are in the Indo-Australian Archipelago, and a few widely distributed species reach India and the Philippines. *Crasodactylus* extends from western India to the Zaire Republic (former Belgian Congo), which is well inside the Ethiopian Region. The subgenus *Anisodactylus* is represented by 1, possibly 2, species in India, Burma, and Indochina but is predominately concentrated in the Palearctic

and Nearctic Regions. The Ethiopian centered subgenus *Progonochaetus* is represented by a single species in tropical India and Burma. And the genus *Pseudognathaphanus* contains 5 species in the Oriental Region but also has 2 on Madagascar.

As defined by Wallace (1876), the Australian Region consists of Australia, Tasmania, New Guinea, New Zealand, New Caledonia, the Celebes and various small islands located to the east of the Celebes and to the north and east of Australia. Some zoogeographers (such as Darlington, 1957) prefer to treat New Zealand and New Caledonia as simply adjacent islands rather than as part of the Australian Region. This is because of the supposed antiquity of these islands and because of the high rates of endemism in animal groups present on them.

New Caledonia contains no endemic groups of Anisodactylina. However, it does have 1 species of *Anisotarsus* and 2 species of *Gnathaphanus*. These 3 species have presumably recently arrived on New Caledonia by dispersal across present water gaps. *Anisotarsus* is centered primarily in the New World and in Australia and Tasmania. And *Gnathaphanus* is predominately centered in Australia and to a lesser degree in the Indo-Australian Archipelago. With the exception of the 1 species of *Anisotarsus* (presumably derived from Australia rather than the New World), New Caledonia shows no zoogeographical relationships with other major faunal regions and would seem best placed within the Australian Region.

New Zealand contains 4 groups of Anisodactylina; two of these, *Allocinopus* and *Triplosarus*, are endemic. *Allocinopus* has undergone considerable evolution in New Zealand but presumably once shared with *Hypharpax*, *Cenogmus*, and *Crasodactylus* a common ancestor which originated in Australia. *Allocinopus* shows no close relationships with other groups and appears to have been evolving on New Zealand for a considerable period of time. New Zealand also contains 2 species of the New World, Australia and Tasmania centered *Anisotarsus* and 1 species of the Australia and Tasmania centered *Hypharpax*. The presence of 2 endemic, highly evolved, and only slightly related groups on New Zealand suggests long separation. But on the basis of Anisodactylina distributions, New Zealand has a definite zoological relationship with Australia and Tasmania, and it seems best to follow Wallace (1876) and treat New Zealand as a subregion of the Australian Region.

The continent of Africa is clearly divided into Palearctic and Ethiopian Regions by the distribution of groups of Anisodactylina. Except for 1 species of *Crasodactylus*, Africa north of the Sahara Desert contains only Palearctic groups, namely *Anisodactylus*, *Diachromus*, *Pseudodichirus*, *Hexatrachus*, *Pseudhexatrachus* and *Scybalicus*. The Sahara Desert is apparently devoid of Anisodactylines except possibly for the species *Crasodactylus punctatus*, which is reported by Basilewsky (1950) to occur in sandy places from India to the mountains of Kivu in the Belgian Congo. Africa south of the Sahara Desert constitutes the Ethiopian Region minus Madagascar and associated smaller islands. The Ethiopian portion of Africa contains groups which, except probably for *punctatus* of the genus *Crasodactylus*, contain species adapted to tropical habitats. The temperate southern tip of Africa does not appear to have an Anisodactylina fauna. Of the Ethiopian groups: *Crasodactylus* is also found in the Palearctic and Oriental Regions; *Pseudognathaphanus* is centered in the Oriental Region but has 2 species on Madagascar; *Scybalicus* has 2 species in the Palearctic Region; and *Progonochaetus* has 1 species in India and Burma and 37 in the Ethiopian Region. The remaining 3 groups are endemic to the Ethiopian Region.

The presence of distinct Palearctic and Ethiopian faunas of Anisodactylines north and south respectively of the Sahara Desert suggests that this desert serves as a good boundary between the Palearctic and Ethiopian Regions. Ball (personal communication) has commented on the effectiveness of the Sahara Desert as a barrier to dispersal of carabids in general. The Sahara Desert is similarly effective in barring dispersal of birds, plants, and butter-

flies, but it is not effective in barring dispersal of mammals as much of the Palearctic part of Africa is inhabited primarily by Ethiopian forms. (Moreau, 1966).

Wallace (1876) treated Madagascar as a subregion of the Ethiopian Region. Madagascar possesses 2 groups of Anisodactylina, *Pseudognathaphanus*, with 2 species endemic to Madagascar and 5 in the Oriental Region, and *Progonochaetus*, with 3 species endemic to Madagascar, 34 on the Ethiopian portion of Africa, and 1 in the Oriental Region. Madagascar thus has equal zoogeographic relationships with the Ethiopian portion of Africa and with the Oriental Region. Geographically, the best placement of this island is probably as a subregion of the Ethiopian Region, but with regards to the Anisodactylina fauna it could almost as well be treated as a subregion of the Oriental Region.

The groups occurring in the Nearctic Region are predominately centered in temperate and warm temperate areas of the eastern portion of North America. Six groups, *Spongopus*, *Pseudaplocentrus*, *Geopinus*, *Xestonotus*, *Amphasia*, and *Pseudamphasia*, form a subtraction pattern towards the west and are confined to the eastern United States and southeastern Canada. The subgenus *Gynandrotarsus* is centered in the eastern United States but has some species in the western part and in temperate areas of Mexico. The subgenus *Anisotarsus* is centered in northern Mexico, is moderately abundant in number of species in the eastern United States and southeastern Canada, and is poorly represented in the western United States. Three groups, *Anisodactylus*, *Anadaptus*, and *Aplocentrus*, are equally well represented in both eastern and western United States or in eastern and western portions of southern Canada. The genus *Dicheirus* is restricted to the western half of North America.

The Neotropical Region contains only 5 groups, 1 of which is shared with the Nearctic. The shared group, *Anisotarsus*, is centered in temperate and warm temperate areas of the Australian, Nearctic and Neotropical Regions but in the latter 2 regions has a few species which extend along the tops of mountains into areas whose lowlands are tropical. The distribution of Anisodactylina within the Neotropical Region strongly supports Wallace's (1876) division of it into tropical and temperate subregions. Three of the 4 endemic groups of the Neotropical Region, *Criniventer*, *Pseudanisotarsus*, and *Anisostichus* are apparently restricted to temperate areas in southern South America. The 4th, *Notiobia* (*s. str.*), is restricted to tropical areas. As discussed above, the subgenus *Anisotarsus* within the Neotropical Region is centered in temperate and warm temperate areas and extends into tropical areas only along mountain tops. The Anisodactylina fauna of the Neotropical Region thus is composed of distinctly tropical (1 group only) and temperate elements (4 groups).

The distribution of groups of Anisodactylina does not offer much support to the concept discussed by Kuschel (1963) of combining temperate southern South America, temperate southern Africa, and the Australian Region into a single Austral Region. The only close relationship among Anisodactylina in these areas is the occurrence of *Anisotarsus* in both the New World and the Australian Region. The 3 endemic genera in temperate southern South America share no close relationships with the 3 endemic groups in the Australian Region. And temperate southern Africa does not appear to contain an Anisodactylina fauna.

The supra-specific taxa of Anisodactylina were analyzed to determine whether groups are more abundant in temperate or in tropical regions. Table 7 (p. 443) divides the groups into those found in temperate and tropical habitats. In the preparation of this table, the distribution of species in each group was compared with climate and vegetation region maps in the Hammond 1967 World Atlas and Gazetteer. Groups containing both tropical and temperate adapted species were marked under both the temperate and tropical columns. Species inhabiting mountain tops in areas with tropical lowlands were classified as temperate adapted despite the tropical conditions of surrounding lowlands. I am aware that the climate of mountain tops in tropical areas is not completely equivalent to that of temperate areas, but

species living there are exposed to colder conditions and also probably to less biotic competition as are species in "true" temperate areas. A result of this method of classification is that *Chydaeus* is considered as a temperate rather than a tropical group because its species are apparently restricted to mountainous areas within the tropics. And *Anisotarsus* is treated as a completely temperate group although several of its species are found on mountains in areas with tropical lowlands.

Table 7 (p. 443) indicates that a total of 30 groups are found in temperate habitats, and that 26 of these groups are restricted to such habitats. Only 11 groups are found in tropical habitats, and 4 of these groups are also found in temperate ones. The subtribe Anisodactylina is clearly more abundant in number of groups in temperate than in tropical areas. A likely explanation for this is that Anisodactylines originated in temperate areas (as postulated in the phylogeny section) and are as yet in general less adapted to tropical habitats.

One might ask whether the greater number of supra-specific taxa in temperate areas results from the fauna of these areas being better known. This might in part be the answer. However, the fauna of tropical Africa is certainly at least moderately well known but contains only 4 endemic and 3 nonendemic groups, while the fauna of the Nearctic Region contains 10 endemic and 2 nonendemic groups. And South America contains 4 temperate adapted groups (3 of which are endemic) and only a single tropical adapted one. Temperate portions of South America are no better collected than tropical ones.

Table 6 (p. 440) presents information on the number of species in each of the 6 faunal regions and information on the average number of species per taxon in each such region. The table indicates that in terms of average number of species per group, the 6 faunal regions rank moderately well according to the postulated sequence of evolution and dispersal of Anisodactylines, that is, areas presumed to have older Anisodactylina faunas tend to have more species per supra-specific taxon. For example, the Australian Region which is the presumed origin of Anisodactylina ranks first with an average of 12.7 species per group while the Oriental Region ranks last with 3.3 species per group. The probable reason for areas with older Anisodactylina faunas having more species per group is explosive radiation of supra-specific taxa immediately after colonization followed by evolution of additional species in the already evolved groups. Thus, the number of species per group would increase according to the age of the Anisodactylina fauna.

The low values for the Palearctic and Nearctic Regions may be due not only to their Anisodactylina faunas being relatively young but to extinction of many species during glacial periods of the Pleistocene. Some supra-specific taxa no doubt also became extinct during such periods, but their percentage of extinction may have been much less than that for species. A greater percentage of species extinction during glacial periods may explain the low value for the large Palearctic Region, which presumably has a slightly older Anisodactylina fauna than the Nearctic Region, yet only approximately half as many species. A possible explanation for such greater species extinction in the Palearctic Region is the differing arrangement of mountains. The mountains of the Nearctic Region run predominately from north to south and thus probably did not greatly hinder movement of species southward into refugia during Pleistocene glacial periods. In contrast, mountains of Eurasia run predominately east to west and therefore probably prevented southward movement of many species during glacial periods.

#### Contemporary Zoogeography of the Subgenus *Anisotarsus*, Especially in North America.

Within the New World the subgenus *Anisotarsus* is generally amphitropical in its distribution, being centered in temperate to warm temperate areas of North and South America (Fig. 132). Thirteen species are found in North America, and only 2 of these, *terminata* and *mexi-*

*cana*, extend into Central America. The other 11 species extend no farther south than the edge of the Mexican plateau in the Golfo de Tehuantepec region. And except for *lamprota* which possibly occurs in tropical areas along the eastern coast of central Mexico, these 11 species are found in areas with a temperate or warm temperate climate. Specimens of *terminata* found south of the Mexican plateau are restricted to highland and mountain regions of 1,000 feet or higher which presumably are warm temperate or temperate in climate. The species *mexicana* is similarly restricted except for 2 males recorded from Merida, Yucatan, Mexico. The species in South America show a similar temperate and warm temperate distribution except for *chalcites* and *amethystina* which occur in tropical areas. All other South American forms are restricted either to temperate and warm temperate areas in the central part of the continent or to the Andes and other elevated non-tropical areas in the northern part. None of the South American species extend into Central America.

It is interesting that *lamprota*, *chalcites* and *amethystina*, which possibly occur in tropical environments, and *mexicana*, which extends into Central America along mountains and highlands, constitute the *mexicana* lineage. As discussed in the sections on phylogeny and historical zoogeography, this is the only instance in which North and South American species of *Anisotarsus* show close phylogenetic connections.

The distribution of each of the 13 North American species is shown by dots on separate maps for each species. In Fig. 253 the ranges of all the species are each delimited by a line drawn around the outermost dots for each species. This figure shows that species are most numerous in southwestern Texas, northern and Central Mexico, less numerous in the eastern half of North America, few in western United States, and absent north of the fiftieth parallel. Further, the 3 species found in California, Arizona, and New Mexico are merely northward extensions of species primarily centered in Mexico. These 3 species are restricted to mountains in Arizona and New Mexico, while the single one reaching California, *purpurascens*, is found there along the coast and in mountains or other elevated areas of the interior. The eastern part of the United States north of the Gulf region contains 4 species, 3 of which are widespread. This suggests that the area presently lacks effective barriers to dispersal of species within it. It also has certain implications concerning historical zoogeography which are discussed in that section.

It is also evident from Fig. 253 that the subgenus in North America is primarily adapted to temperate and warm temperate environments with summer rains. Species do not extend far north of the Canadian border, and the 3 that are found north of the border are all wide ranging and centered in warm temperate areas. The decrease in number of species northward is probably due to effects of Pleistocene glaciation (Howden, 1969), and also to a lack of tolerance for cold environments. Only 2 species enter the tropics of Central America, and these 2 species (except for the single *mexicana* from Merida) are restricted to mountains and highlands which presumably have subtropical or even temperate climates. The decrease in species towards the west within the United States is correlated with decreasing summer rainfall. For example, Arizona which receives summer rainfall has 3 species while California which very rarely receives summer rainfall has only 1 species.

The species *flebilis* has a disjunct distribution which possibly is also correlated with the amount of summer moisture. It occurs on Guadalupe Island, southern Baja California, and the Mazatlan region of western Mexico. Guadalupe Island has a persistent summer fog belt in the summit section (Axelrod, 1967) and has a milder and moister climate than the immediately adjacent mainland (Savage, 1967). The persistent summer fogs and milder and moister climate probably are analogous in their effects to summer rain. I suspect that all specimens recorded from Baja California actually were collected in Lagunan woodland areas of the Laguna Mountains which have a cooler, moister climate than the surrounding low-



lands (Axelrod, 1958). And the Mazatlan region also receives summer rains.

The distribution of species has a limited correlation with topography. Species occurring in Mexico are primarily centered in the highlands while those found in New Mexico and Arizona are restricted to mountains or the foothills of mountains. In the warm temperate eastern United States species range over mountains and rivers which are barriers to other groups of Carabidae. The Rocky Mountains in the western United States may possibly serve as a barrier, but decreasing summer rainfall is probably a more important factor.

Central America contains only 2 known species of *Anisotarsus*. Erwin (1970) working on *Brachinus* also found a marked reduction in the number of known species from this area and concluded this is probably due to under-collecting. I feel, however, that the great reduction of number of known species of *Anisotarsus* from Central America is due rather to lack of adaptation to tropical environments. A total of 7 species of the subgenus *Notiobia* are recorded from this area. The species of both *Anisotarsus* and *Notiobia* tend to be found under debris on the ground, and if *Anisotarsus* species were numerous in Central America they should have been collected along with *Notiobia*. I personally have collected in Costa Rica, primarily in the lowlands, but did not encounter any *Anisotarsus* there.

Table 8 (p. 445) provides a list of the range extent determined for each species by a linear measurement between the 2 most distant localities on its distribution map. Thirty-one percent of the species have range extents less than 501 miles; 23 percent have ranges less than 1,001 miles; 31 percent have ranges of 1,001 to 2,000 miles; and 15 percent have ranges greater than 2,000 miles.

Ball and Freitag (in Freitag, 1969) and Erwin (1970) attempted by correlating species distributions to define centers of concentration for use in conjunction with a discussion of historical zoogeography of the species of their respective groups. To do this, Ball and Freitag, working on *Evarthrus*, which are flightless, excluded wide ranging species and those found on both sides of major barriers. Erwin working on the less barrier restricted *Brachinus*, which do fly, excluded species with ranges of over 1,000 miles. Since most species of *Anisotarsus* fly and are less barrier restricted than *Evarthrus*, I chose to follow Erwin and exclude species with ranges over 1,000 miles. This eliminated southern Texas as a possible center of concentration since the high number of species found there is primarily due to the overlapping of edges of widespread species. Also it eliminated the eastern United States.

Only 1 center of concentration can be delimited for *Anisotarsus* in North America. This is in central Mexico and contains 5 species with ranges less than 1,000 miles. In contrast, Ball and Freitag found *Evarthrus* has 8 centers of concentration, all in the eastern United States, while Erwin concluded that *Brachinus* has 8 in North and Central America combined. The absence of further centers of concentration in *Anisotarsus* is due in part to the smaller size of this group and in part to past species extinctions which have obscured centers of evolution.

### Historical Zoogeography of the Subgenus *Anisotarsus*.

Since fossils are not known for this group, conclusions must be drawn from analyses of current distribution patterns of species, of the likely phylogeny of the group, and of information concerning past fluctuations in climate and flora. Because South American and Australian Region forms are not well known, this section deals mainly with the species of North America. The following sources have been consulted: Auffenberg and Milstead (1965); Axelrod (1948, 1958, 1959, 1967); Ball (1964, 1966); Ball and Freitag (in Freitag, 1969); Blair (1958, 1965); Darlington (1965); Dietz and Holden (1970); Dorf (1960); Erwin (1970); Graham (1964); Hopkins (1967); Howden (1969); King (1958); Larson (1969); MacGinitie (1958); Martin (1958); Martin and Mehninger (1965); Raven (1967);

Ross (1965); Smith and Hallam, (1970); Whitehead (1965); Wolfe (1969); and Wolfe and Leopold (1967).

In the early or middle Tertiary a species of *Anisotarsus* dispersed to North America by crossing water gaps between various islands in the present Central American and Caribbean areas. This species ultimately produced all of the North American *Anisotarsus* fauna except those of the *mexicana* lineage. This early crossing into North America is strongly suggested by the fact that except for the *mexicana* lineage the North and South American species of *Anisotarsus* do not show any close phylogenetic relationships.

The *mexicana* lineage is composed of 4 named forms. Three of these, *lamprota*, *chalcites*, and *amethystina*, seem to be adapted to or at least tolerant of tropical conditions although further field collecting and work needs to be done to verify this conclusion. The fourth form, *mexicana*, is adapted to mainly temperate or warm temperate conditions but extends far into Central America along mountains and highlands. The *mexicana* lineage is the only lineage common to both North and South America, its forms are all closely related, and 3 of its forms have tropical adaptations or tolerances. These facts suggest that the ancestor of the North American forms migrated north into North America via Central America after this area connected North and South America in the Pliocene. It is not probable that this migration took place earlier in the Tertiary because the *mexicana* lineage has several apomorphic characteristics suggesting recent evolution. And, the North and South American species undoubtedly would have diverged and lost their close relationship if isolated in the 2 continents earlier in the Tertiary before land connections were established.

It is difficult to reconstruct in detail the past zoogeographic history of the remaining North American *Anisotarsus*. The most productive approach is to determine the past history of individual species, groups of related species, and groups of species with similar contemporary distribution patterns.

The postulated phylogeny for New World *Anisotarsus* suggests that initial production of North American forms took place somewhere in Mexico. The species *brevicollis* is today centered in temperate and warm temperate Mexico and extends north into the southwestern United States. It is the sole extant member of the *brevicollis* lineage, which has no apparent synapomorphies with other lineages. On the basis of chorology its closest relative appears to be the *cyanippa* lineage which is restricted to central Mexico.

The *cyanippa* lineage is composed of the sister species *hilariola* and *cyanippa*, with the flightless *hilariola* known only from the vicinity of Chilipancingo and Omiltemi in Guerrero, and the usually flightless *cyanippa* recorded only from Jalisco, Morelos, and Nayarit. Since the 2 are closely related, and their ranges appear to be slightly disjunct, they probably arose from a common ancestor whose range in central Mexico was contracted by events during the Pleistocene.

The sister species *nitidipennis* and *schlingeri* show north-south vicariance, with *nitidipennis* occurring in the United States and Canada, and *schlingeri* being found in central Mexico. Presumably they had a common ancestor whose range was split into north and south components by Pleistocene events. The northern component became adapted to temperate conditions and gave rise to *nitidipennis* while the southern component became adapted to warm temperate conditions and produced *schlingeri*.

The species *virescens* and *picea* do not show close relationships to other species and little can be deduced about their past history except that their close relatives are now extinct.

The species *flebilis*, *purpurascens*, *mexicana* and *brevicollis* each have a disjunct distribution best explained by events of the Pliocene and Pleistocene. The species *flebilis* is restricted to Guadalupe Island, southern Baja California, and the Mazatlan region of western Mexico. The species *purpurascens* is found in coastal and highland areas of California, in

mountains surrounded by desert in Arizona, and in areas of various altitudes in Mexico and along the Gulf in southern United States. And *mexicana* and *brevicollis* are both centered in mainland Mexico but have disjunct populations in desert isolated mountains of Arizona, New Mexico, and southern Baja California.

The following climatic, floral, and geological events serve to explain the disjunct distributions of these 4 species. During Miocene and early Pliocene, Madro-Tertiary woodland and chaparral ranged widely over the lowlands of western United States, Baja California, and into Mexico (Axelrod, 1948, 1958, 1963). In late Pliocene and Pleistocene, the major mountain systems of North America, including the Sierra Nevada, Coastal Ranges of California, Transverse and Peninsular Ranges of California, Cascades of Oregon and Washington, Basin Ranges of Nevada, central and southern Rockies, and the Sierra Madres of Mexico, assumed their present heights (Axelrod, 1958). Volcanic activity in late Miocene formed a series of volcanoes extending along the present east coast of Baja California from the southern San Pedro Martirs in the north to the Cape Region at the south (Axelrod, 1958). These geological events were accompanied by, and in part produced, a continued decrease in yearly rainfall over lowland areas, a shift in the western United States and northwestern Mexico to a seasonal distribution of rain mainly in the winter, general lowering of winter temperature, and greater extremes of temperature (Axelrod, 1948, 1958, 1963, 1967).

The elevation of the Sierra Nevada-Cascade axis and the Peninsula Ranges of southern California along with decreased yearly rainfall produced drier inland climates, and the present desert climax evolved in dry areas of the American southwest. This increasing aridity and desert development during late Pliocene and Pleistocene isolated more mesic plant formations such as woodland on the higher summits of Guadalupe Island, and mountainous areas of Baja California, Arizona, and New Mexico. Today the Guadalupe Island flora contains 164 native vascular plant species, of which 32 are endemic to the island and 24 to this island and the southern California Islands (Raven, 1967). The Sierra Laguna south of La Paz and to a lesser degree the higher parts of the Sierra Gigantea in southern Baja today contain a distinctive woodland termed "Lagunan Woodland" by Axelrod (1958). Many of the late Tertiary fossil plant species of this woodland also occurred at that time in the southwestern United States. Today many of the extant species are endemic while some occur also in the mountains of southern Sonora and Sinaloa (Axelrod, 1958). The Lagunan Woodland is a distinctive derived assemblage of the broader Sierra Madrean Woodland which today ranges across north Mexico from Southern Baja California to the Sierra Madre Oriental in Nuevo Leon and Tamaulipas and northward into southern Arizona, New Mexico and western Texas (Axelrod, 1958).

From the above information on late Tertiary and Pleistocene events, one might infer that *flebilis*, *purpurascens*, *brevicollis*, and *mexicana* were once more widespread over southwestern North America, but then retreated into Mexico and into island and mountain refugia elsewhere with the occurrence of increasing aridity during late Pliocene and early Pleistocene. However, the disjunct populations of these species are little differentiated, and if they had been isolated since late Pliocene or early Pleistocene, they might be more distinct. Desert areas of the southwestern United States were contracted during the ice ages of the Pleistocene. During the maximum ice advance of the Wisconsin period about 20,000 years ago, biotic zone depressions of 900 to 1,200 meters occurred in the southwestern United States, and woodland occupied lowlands in this area which is now again covered by desert or grassland (Martin and Mehringer, 1965). California and Baja California also experienced more mesic conditions and range extensions of woodland flora during Pleistocene glaciations (Axelrod, 1967). Thus, although the 2 species were probably isolated in

their refugia by late Pliocene or early Pleistocene, they presumably were able to spread over lowlands connecting these refugia as recently as the Wisconsin. This explains the lack of divergence of their now disjunct populations.

The species *terminata* contains 4 morphs which while intergrading over broad areas are each centered in distinct geographical areas. The northern, Texas, Florida, and Mexico morphs are respectively centered in: northern North America primarily north of the fortieth parallel; Texas; Florida; and Mexico. The occurrence of these morphs may be explained by Pleistocene events. The northern morph now occurs predominantly in areas with cool temperate climate, and most of the range it now occupies was covered by ice during the maximum Wisconsin ice advance (Howden, 1969). The part of its range not covered by ice at that time appears to have consisted of tundra and taiga or the northern boundary of a boreal forest (Martin, 1958). The northern morph thus has apparently occupied its present range only since Wisconsin.

There have been at least 3 additional earlier glacial periods during the Pleistocene (Howden, 1969). Possibly one or more of these glacial periods pushed populations of *terminata* south and westward and maintained them in a semi-isolated state in areas of the central United States (possibly the southern edge of the present Great Plains). These populations could then have evolved into the present northern morph.

Considerable controversy exists as to the degree of climatic change induced in the southern United States during the Wisconsin and other glacial periods. However, most workers are able to agree that there was at least some change. It is likely that the Wisconsin and almost certainly the 3 earlier glacial periods produced sufficient cooling to force populations of *terminata* into semi-isolated refugia in Florida, northern Mexico, and central or southern Mexico. There is considerable evidence of Floridian and Mexican refugia in other groups of insects (Howden, 1969) and in amphibians (Blair, 1965). The exact location of the presumed central or southern Mexico refugium and the reasons for its postulated semi-isolation cannot be determined until more is known about Pleistocene events in Mexico. Presumably during their periods of semi-isolation, the refugia produced the 4 morphs now found in *terminata*. When the ice ages ended, the morphs then moved into their present ranges.

The postulated central United States refugium produced the northern morph, the Florida refugium the Florida morph, the northern Mexico refugium the Texas morph, and the central or south Mexico refugium the Mexico morph. There is a possibility that the postulated northern Mexico refugium producing the Texas morph might have been located in southern California, Arizona, New Mexico or other areas of southwestern America. However, if this were so, then there would probably be disjunct populations of *terminata* in the mountains of these states. Also the possession of a slender median lobe by the Texas and Florida morphs suggests that the Florida refugium and the one producing the Texas morph were in contact during at least part of their existence. The probable way such contact took place was that the refugium producing the Texas morph was located in northern Mexico and connected to the Florida one by a narrow Gulf Coast corridor. The tendency for the median lobe of Mexico morph specimens to broaden southwards suggests that the refugium producing this morph may have been more isolated from the Florida and northern Mexico ones. However, I do not presently know what climatic or environmental conditions in Mexico could have produced such isolation.

Only 1 center of concentration can today be delimited for *Anisotarsus* in North America, and it occurs in central Mexico. Considerable evolution may have occurred there during late Tertiary and Pleistocene. However, before early Oligocene much of Mexico and southern United States had a tropical climate (Dorf, 1960), and most evolution before then probably

took place in more northern localities.

The eastern United States today contains 5 species, *purpurascens*, *terminata*, *nitidipennis*, *picea*, and *maculicornis*. The first species extends no farther north than the Gulf region and is centered mainly in Mexico. The species *terminata*, *nitidipennis*, and *picea* are widespread forms with range extents over 1,000 miles and each extend northward to or slightly beyond the forty-fifth parallel. The species *maculicornis* has a range extent of 750 miles and is more numerous and primarily concentrated around the Gulf region and associated lowlands. The distribution of species in the eastern United States and Canada suggests that the maximum periods of Pleistocene glaciation had a devastating effect on *Anisotarsus* of these 2 areas and pushed species south or southwest or exterminated them. It is reasonable to postulate that if maximum glacial periods had not had such a devastating effect, then the unglaciated areas of the eastern United States would have several localized species as does Mexico. The species *terminata*, *nitidipennis*, and *picea* appear to be vagile forms which have only recently spread northward from possible southern refugia or centers of evolution. And *maculicornis* may also be a species now extending its range northward.

The species of *Anisotarsus* in the Australian Region are little differentiated from those in the New World. Australia and Antarctica were connected until some time in Tertiary (Dietz and Holden, 1970; Smith and Hallam, 1970). And from late Cretaceous to Miocene, *Nothofagus* and certain other plants occurred on the present day Antarctica Peninsula and possibly elsewhere on the continent (Darlington, 1965). The juncture of Australia and Antarctica and the presence of plants at least on the Antarctica Peninsula suggest that *Anisotarsus* could easily have dispersed to Australia as recently as Eocene or early Miocene. This would account for the similarity of species of the Australian Region and New World.

#### Zoogeography of the Subgenus *Notiobia*.

A detailed discussion of the zoogeography of the species of *Notiobia* (*s. str.*) is not possible until more is known about the Central and South American forms; a few general comments will be made here. The subgenus is Neotropical (Fig. 146) with its species apparently confined to tropical areas. A few Mexican species extend into areas such as montane cloud forests which might be classified as subtropical rather than tropical. The subgenus may have 3 centers of concentration: southern Mexico with 9 species, 6 of which extend south into Central or South America; Central America which has probably 10 or more species, some of which extend into Mexico or South America; and South America which probably contains more than 20 species. In Figure 146 much of the interior of Brazil and northern South America lacks dots indicating presence of *Notiobia* (*s. str.*). I have seen specimens at various museums from these interior regions but have not recorded the exact localities of such specimens. This will be done in a forthcoming revision of the Central and South American species of the subgenus *Notiobia*.

#### Contemporary Zoogeography of the Subgenus *Gynandrotarsus*.

Climatological data used to explain current distributions are taken from the 1941 Yearbook of Agriculture and Leopold (1959). The distribution of each of the 10 species is shown by dots on separate maps (Figs. 157-166). In Fig. 254 the ranges of all the species are each delimited by a line drawn around the outermost dots for each species. The circles shown in Fig. 254 depict widely disjunct collections each based on a single known specimen of: *opaculus* from Yuma, Arizona; *merula* from Anaheim, California; *dulcicollis* from Los Angeles County, California and from the Huachuca Mountains of Arizona. Since these disjunct collections occur in fairly well collected areas far removed from the species main range, the specimen in question of each species may have been mislabeled.

Figures 157-166 and 254 indicate that species of *Gynandrotarsus* are most numerous in the south central United States (in an area between approximately the thirtieth and fortieth parallels and the ninetieth and one hundredth meridians), and in the United States east of the Mississippi River as 7 species are found in each area. Mexico is strikingly poor in number of species with only *anthracinus* and *darlingtoni* being centered there and *texanus* and *opaculus* extending slightly into it. Florida is also poor in number of species with only *merula* and *haplomus* being widespread there and *rusticus* currently being known only from the Jacksonville area in the extreme northeastern part of the state. The western United States today contains only the single specimens representing the disjunct collections described above and western or northern extensions of species primarily centered in Mexico, east central, or eastern United States. Northern areas also contain few species. Only 3 species are found north of the Canadian border. These 3 are all wide ranging forms primarily centered in more southern latitudes and extend only into the southeastern part of Canada.

It is likely that species of *Gynandrotarsus* are primarily adapted to those temperate and warm temperate environments that receive summer rainfall. The low number of species in Mexico and Florida is possibly explained by lack of tolerance to environments that are warm and humid throughout the year. Also, species found in Mexico are primarily restricted to highland areas receiving frost during the winter. In Florida only *merula* and possibly *haplomus* extend into relatively frost free zones. The decrease in number of species westward seems correlated with decreasing summer rainfall. The decrease in number of species northward is probably due to a lack of tolerance for cold and also in part to the effects of Pleistocene glaciation (see Howden, 1969).

The species distributions have limited correlation with topography. Species found in Mexico are primarily restricted to highland regions which have cooler climates. The species *anthracinus*, which is found in Mexico and the southwestern United States, is in the United States primarily associated with mountainous areas or the foothills of such areas. This pattern probably results from the desert barrier surrounding such elevated areas. In the warm temperate eastern United States, species range over mountains and rivers which are often barriers to other groups of Carabidae (such as the genus *Evarthrus*, Ball and Freitag, in Freitag, 1969).

Table 9 (p. 446) lists the range extents for each species, as determined by a linear measurement between the 2 most distant localities on each species distribution map. (The single specimens representing the disjunct localities of *merula*, *opaculus*, and *dulcicollis* were omitted in range extents determinations. No species have a range extent of less than 500 miles; 30 percent of the species have range extents of 501 to 1,000 miles; 40 percent have range extents of 1,001 to 1,500 miles; 20 percent have range extents of 1,501 to 2,000 miles; and 20 percent have range extents of 2,001 or more miles.

As discussed in detail in the section on contemporary zoogeography of the species of *Anisotarsus*, Ball and Freitag (in Freitag, 1969) and Erwin (1970) attempted by correlating species distributions to define the centers of species concentration. These centers served as data for a discussion of the historical zoogeography of the species of their respective groups. I have done this for *Anisotarsus*; following Erwin, I excluded all species with range extents of over 1,000 miles in my determination of the centers of concentration for this subgenus. On the average, the species of *Gynandrotarsus* are more vagile than those of *Anisotarsus*, and using the 1,000 mile limit would exclude all but 3 species. Therefore, for *Gynandrotarsus* I exclude only those species with range extents of more than 1,500 miles. When this is done, the area between approximately the thirtieth and fortieth parallels and the ninetieth and one hundredth meridians of the south central United States becomes the only center of concentration. It contains 6 of the 10 *Gynandrotarsus* species: *harpaloides*, *opacu-*

*lus*, *texanus*, *dulcicollis*, *ovularis*, and *haplomus*. The single remaining species with a range extent of less than 1,500 miles is *darlingtoni* which is known only from central and northern Mexico. The eastern United States is eliminated as a center of concentration since most of the species found there either have range extents greater than 1,500 miles or are merely extreme eastern extensions of species centered in the south central area described above. The absence of other centers of concentration for *Gynandrotarsus* is perhaps due to the small size of this group, to the high vagility of species, and to extinctions which now obscure the actual centers of evolution.

#### Historical Zoogeography of the Subgenus *Gynandrotarsus*.

The ancestor of *Gynandrotarsus* most likely crossed into eastern North America during late Cretaceous or early Paleocene via the connection with the European part of Eurasia (Fig. 252). Much of North America had a warm or tropical climate in early Tertiary (Axelrod, 1958; Dorf 1960). Extant species of *Gynandrotarsus* are not adapted to a warm climate, and crossing probably took place along the northern portions of the eastern North America-Eurasia connection. Initial evolution in eastern North America also probably occurred in areas of Alaska, Canada, and the northern United States which today lack species of *Gynandrotarsus*.

The 4 species of the sister *harpaloides* and *texanus* lineages are all centered in the south central United States. This suggests that the evolution of these 2 lineages from a common ancestral stock occurred there. Since this area had a tropical or very warm climate before early Oligocene (Dorf, 1960), such evolution probably did not occur until Oligocene or later.

The sister species of the *harpaloides* lineage have a degree of spatial and ecological vicariance. The species *harpaloides* is found (Fig. 159) in the central United States and apparently extends no farther south than northern Texas and northern Louisiana. And *opaculus* occurs (Fig. 158) in the central United States and extends south into northern Mexico. The limited ecological data available suggest that *opaculus* may occur primarily in, or have greater tolerance to, semi-arid conditions such as scrub desert; and possibly *harpaloides* is restricted to more mesic areas. If *opaculus* occurs in both mesic and semi-arid areas and *harpaloides* in mesic areas, then the 2 species have probably been in existence long enough to develop mechanisms enabling them to coexist in the same ecological zone. If *opaculus* is restricted to arid regions and *harpaloides* to mesic areas, then probably the 2 species have not been in existence long enough to successfully invade each other's ecological zones. Also *opaculus* possesses prominent dorsal microsculpture while *harpaloides* and the 2 species of the *texanus* lineage have reduced dorsal microsculpture. This suggests that *opaculus* is the end product of a series of species evolving from the *harpaloides* stock if reduced dorsal microsculpture is regarded as plesiomorphic for the *harpaloides* and *texanus* lineages. If reduced dorsal microsculpture is apomorphic, then *opaculus* is either relatively old or else a species simply retaining a plesiomorphic character state. As discussed in the section on phylogeny, *opaculus* is the closest relative of *harpaloides*. In the absence of additional information, *harpaloides* and *opaculus* probably evolved during the climatic changes of the late Pliocene or early Pleistocene.

The ranges (Figs. 164, 165) of the sister species *texanus* and *dulcicollis* of the *texanus* lineage overlap in Texas, but *texanus* is found only in the southern part of the United States and in northern Mexico while *dulcicollis* is found not only in the south but also as far north as Nebraska, Iowa, and Ohio. The two species thus have at least limited spatial vicariance. They also have a degree of ecological vicariance since available data indicate that *texanus* is restricted to dry semi-desert environments while *dulcicollis* is found in more mesic environ-

ments such as green pastures, orchards, cultivated lands, and grassy areas. These spatial and ecological vicariations suggest that the 2 species arose relatively recently from a common ancestor; *texanus* is found in arid semi-desert regions which likely did not evolve until late Pliocene-early Pleistocene (Axelrod, 1948, 1958, 1963, 1967), and these 2 species probably therefore evolved in late Pliocene or early Pleistocene.

The species *haplomus* belongs to a monotypic branch, has several apomorphic features unique in *Gynandrotarsus*, and is not closely related to other extant species. The unique apomorphic features suggest it evolved before the Pleistocene, but since *haplomus* has a range (Fig. 166) extending across much of the United States, its place of origin can not be elucidated.

The species *rusticus* belongs to a monotypic lineage, is not closely related to other extant species, and occurs (Fig. 162) across all of the eastern United States and in southeastern Canada. Its place and time of origin can not be elucidated without further data.

The species *merula* and *anthracinus* which are closely related on morphological grounds exhibit spatial vicariance: *merula* is found (Fig. 161) in southeastern Canada and in the eastern United States as far west as central Texas; *anthracinus* is found (Fig. 160) in the Davis Mountains of extreme southwestern Texas, mountainous or elevated areas of New Mexico, Arizona, possibly California, and in the highlands of northern and central Mexico. The 2 species have limited ecological vicariance, with *anthracinus* presumably adapted to warmer and possibly more arid environments. Their morphological features and their spatial and possible ecological vicariance suggest that these 2 species have only recently evolved from a common ancestor. Most likely, increasing aridity during Pliocene split the range of their common ancestor into northern and southern components.

The populations of *anthracinus* in the southwestern United States are separated by desert. Despite this, the populations associated with various mountainous or elevated areas exhibit no apparent differentiation. This may be due partly to the vagility of this species, but I feel past Pleistocene climatic changes are the main cause of this lack of differentiation. During Pleistocene glacial periods, desert areas of the United States were contracted, and populations of *anthracinus* were thereby brought into contact with each other. The last period of such contact occurred approximately 20,000 years ago during the maximum ice advance of the Wisconsin. At this time, biotic zone depressions of 900 to 1,200 meters occurred in the southwestern United States, and woodland then occupied lowlands now covered by desert or grassland (Martin and Mehringer, 1965). At this time, and also during earlier ice ages, populations of *anthracinus* moved down from mountainous or elevated areas and occupied all present desert areas.

The apparent absence of *darlingtoni* from mountainous and elevated areas of the southwestern United States which contain refugial populations of *anthracinus* and of other carabids suggests that *darlingtoni* evolved in Mexico and was never present in the United States. The time of its evolution cannot be elucidated without further data. The species *ovularis* is centered in the plains area of the United States (Fig. 163) and possibly evolved there as a result of floral shifts induced by Pleistocene climatic changes.

Only 1 center of concentration can be determined for *Gynandrotarsus*, in the south central United States. Before early Oligocene this area had a tropical or warm climate (Dorf, 1960), and earlier evolution of *Gynandrotarsus* probably took place in more northern localities. However, after early Oligocene, considerable evolution of species occurred in the south central United States; four species of the *texanus* and *harpaloides* lineages seem to have evolved there. The species *merula* extends into the south central center of concentration while its sister species *anthracinus* is found to the west and southwest. Possibly, the common ancestor of these 2 species occupied at least part of the present center of concen-



tration and also extended west and south into the present range of *anthracinus*. Presumably, Pliocene events subsequently divided the range of this species, thus allowing evolution of *anthracinus* and *merula*.

Today there are 7 species in the United States east of the ninetieth parallel. Two of these, *harpaloides* and *opaculus*, are centered in the south central United States. The species *ovularis* is widespread with a range extent of 1,500 miles, is found only as far south as approximately the thirty-fifth parallel, and is centered in the north central grasslands of the United States. The remaining 4 species, *haplomus*, *rusticus*, *merula*, and *dulcicollis* all have range extents of more than 1,400 miles and are most concentrated or abundant in central or southern latitudes of the United States. The distribution of species in the eastern United States suggests that the maximum periods of Pleistocene glaciations had a devastating effect on most of the then extant species, pushing them south or southwest or exterminating them. If maximum glacial periods had not produced such a drastic effect, then the unglaciated areas of the eastern United States would probably have several more localized species as does the south central United States. The species *rusticus*, *merula*, *dulcicollis*, and *haplomus*, are vagile forms which may only recently have spread northward from possible southern refugia or centers of evolution.

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Table 1. Color combinations of Panamanian morph of *Notiobia parilis*.

Locality	Color Combinations				
	I	II	III	IV	V
Barro Colorado, Panama	2 ♂♂, 8 ♀♀	2 ♂♂, 2 ♀♀	2 ♂♂		
Bugaba, Panama	1 ♂				
Archipelago de las Perlas, Panama	1 ♀				
La Caja, 8 Km W. San Jose, Costa Rica	1 ♂	1 ♂, 1 ♀	1 ♂		
San Jose, Costa Rica		3 ♂♂, 1 ♀		2 ♂♂, 1 ♀	
Turrialba, Costa Rica					1 ♂
Costa Rica			1 ♀		

I = head and pronotum predominantly green but with slight cupreous tinge, elytron purplish.

II = head and pronotum predominantly cupreous but with slight greenish tinge, elytron purplish.

III = head and pronotum predominantly aeneous but with slight cupreous and/or greenish tinge, elytron purplish.

IV = head and pronotum bluish green, elytron bluish purple.

V = head, pronotum, and elytron bluish green.

Table 2. Plesiomorphic and apomorphic character states used in Figs. 240, 241.

No.	Character	Character State	
		Plesiomorphic	Apomorphic
<b>Color</b>			
1	of body and dorsum	body rufopiceous to black, dorsum lacking metallic tinges	dorsum of many specimens with metallic tinges present (a) dorsum with metallic tinge always present (b) dorsum brightly bi-colored (c) dorsum brightly tri-colored (d) dorsum pale rufotestaceous except for median darker areas (e) entire body depigmented
<b>Microsculpture</b>			
2	of dorsum	not causing iridescence	causing iridescence
3	of pronotum	isodiametric mesh	very fine dense lines
4	of elytron	isodiametric mesh	obsolescent except at apex
5	of elytron	granulate slightly transverse mesh not causing iridescence	extremely fine dense lines causing iridescence
<b>Body Pubescence</b>			
6		generally absent	venter and dorsum of head and pronotum and part or all of elytron pubescent (a) all of body pubescent
<b>Head</b>			
7	frontal fovea	not obsolescent	obsolescent and obscured by punctures
8	clypeo-ocular prolongation	absent	present in most species (a) present in all species
9	fronto-clypeal suture	unmodified	very deep and prominent, obliterating frontal fovea

Table 2. Plesiomorphic and apomorphic character states used in Figs. 240, 241. (continued).

No.	Character	Character State	
		Plesiomorphic	Apomorphic
10	eye	normal	large and bulging
11	gena	wide	narrow
12	antennal sulcus	absent	present
13	mandible	unmodified	apex striate dorsally (a) elongate and striate dorsally
14	1 seta at each side of mentum	present	absent
15	mental tooth	moderate tooth present	absent (a) moderate tooth present (b) very prominent tooth present
16	mentum and submentum	completely separate	free medially in all specimens but fused laterally in most specimens (a) completely fused
17	ligula apex	not to slightly expanded laterally	moderately to strongly expanded laterally. (a) not to slightly expanded laterally
18	setae on paraglossa	absent	present on dorsum and lateral margins (a) present in most species on dorsum and/or lateral margins
19	Pronotum shape	semi-rectangular, with side slightly to moderately curved towards posterior angle	orbiculate (a) cordate (b) cordate, with side strongly sinuate before posterior angle

Table 2. Plesiomorphic and apomorphic character states used in Figs. 240, 241. (continued).

No.	Character	Character State	
		Plesiomorphic	Apomorphic
20	posterior angle	slightly obtuse to slightly acute	strongly rounded (a) very acute and outward projected
21	lateral depression	lacking sharply delimited lateral depression	with sharply delimited lateral depression
22	apparent inflexion of integument	absent	integument with apparent inflexion at edge of lateral depression
23	apical bead	present at least laterally	absent
24	no. lateral seta each side	1	2
25	non-setigerous punctures	absent or very few	numerous, small dense punctures present
26	pubescence	absent	present along lateral part of apex (a) present along sides and lateral part of base and apex
<b>Legs</b>			
27	Forefemur of ♂	lacking tooth on inner margin	with tooth on inner margin in most ♂♂
28	Foretibia	unmodified	apical portion strongly expanded laterally and with large excavate dilation at external apex
29	Foretibia of ♂	inner proximal margin only very slightly emarginate	inner proximal margin moderately emarginate (a) inner proximal margin strongly emarginate
30	Foretibial apical spur	lanceolate	trifid

Table 2. Plesiomorphic and apomorphic character states used in Figs. 240, 241. (continued).

No.	Character	Character State	
		Plesiomorphic	Apomorphic
31	Hindtibial apical spur	lanceolate	spatulate
32	segments II to IV of hindtarsus of both sexes and segments II to IV of fore- and midtarsus of ♀	unmodified	with dense ventro-lateral cover of somewhat thickened setae
33	hindtarsus	not shortened, first segment 3 or more times long as wide	shortened, first segment 2 or less times long as wide in most specimens
<b>Elytron</b>			
34	scutellar stria	unmodified	absent or vestigial
35	dorsal non-setigerous punctures	absent	row present on odd and in some specimens also even intervals (a) all intervals with small, dense punctures
36	dorsal setigerous punctures on intervals	1, rarely 2, on III	3 to many on III (a) row of punctures extended towards base on III (b) row of punctures on III, V, VII
37	stria	evenly rounded, not deep and prominent	semi-rectangular in form, deep and prominent
<b>Abdomen</b>			
38	extra setae on sterna	absent	present in some (a) present in all specimens of both sexes
39	no. ambulatory setae on sternum VI of ♀	4	2



Table 2. Plesiomorphic and apomorphic character states used in Figs. 240, 241. (continued).

No.	Character	Character State	
		Plesiomorphic	Apomorphic
40	apex sternum VI of ♀	unmodified	with slight semi-plate like swelling medially (a) with prominent plate like swelling medially
41	<b>Male genitalia</b> median lobe	symmetric	asymmetric
42	apical disc of median lobe	absent	very slight disc (a) small disc (b) moderate sized disc (c) "button" shaped disc
43	<b>Female genitalia</b> valvifer	moderately sclerotized, not vestigial, lateral margin discrete	lateral margin semimembranous and not discrete (a) vestigial
44	valvifer	triangular in form and with distal setae	subtriangular in form and with distal setae (a) subtriangular in form and lacking distal setae (b) subtriangular in form, lacking distal setae, with concave area at distal margin
45	valvifer	triangular in form and not lobed	lobed
46	segments of stylus	separate	fused
47	setae on basal segment of stylus	absent	1 or 2 small setae on distal lateral margin in many specimens (a) 1 or 2 small indistinct setae on distal lateral margin (b) 1 or 2 (rarely 3) short setae on distal lateral margin (c) 2 or more prominent long setae on distal lateral

Table 2. Plesiomorphic and apomorphic character states used in Figs. 240, 241. (concluded).

No.	Character	Character State	
		Plesiomorphic	Apomorphic
47			margin (d) setae on distal lateral and mesal mar- gins
48	extra setae on apical segment of stylus	absent	present
49	apical seg- ment of stylus	unmodified	elongate in most spec- imens
50	stylus	unmodified	moderately dilated lat- erally, lateral margin of apical segment finely serrate and with very small spines arising from between indentations (a) strongly dilated later- ally, lateral margin of ap- ical segment serrate and with short stout spines arising between serrations
51	proctiger	unmodified	modified into discrete sclerite (a) modified into paddle shaped sclerite free distal- ly from tergum (b) absent
52	<b>Habitat</b> climate of habitat	generally temperate	generally tropical

Table 3. Convergent character states among genera and subgenera of the subtribe Anisodactylina.

Character state	Taxa
clypeo-ocular prolongation present	<i>Criniventer</i> ; 1 sp. of <i>Crasodactylus</i> ; <i>Cenogmus</i> ; some spp. of <i>Hypharpax</i> ; some specimens of species of <i>Scybalicus</i> ; common ancestor of <i>Notiobia</i> and <i>Diatypus</i> ; ancestor of Anisodactyloids.
eye large and protruding	some species of <i>Anisotarsus</i> ; common ancestor of <i>Notiobia</i> and <i>Diatypus</i> ; <i>Phanagnathus</i> ; <i>Pseudaplocentrus</i>
narrow gena	some species of <i>Anisotarsus</i> ; common ancestor of <i>Notiobia</i> and <i>Diatypus</i> ; <i>Phanagnathus</i> ; <i>Pseudaplocentrus</i>
mentum and submentum completely fused	<i>Anisostichus</i> ; Anisodactyloids except <i>Progonochaetus</i>
ligula apex expanded laterally	some specimens of <i>Notiobia</i> ( <i>Anisotarsus</i> ) <i>tucumana</i> ; "Paradiatypus" species group of <i>Diatypus</i> ; <i>Criniventer</i> ; <i>Rhysopus</i> ; ancestor of all temperate adapted Anisodactyloids (except for <i>Xestonotus</i> )
2 pronotal lateral setae on each side	<i>Progonochaetus</i> ; <i>Diachromus</i>
trifid foretibial apical spur	3 species of subgenus <i>Anisodactylus</i> ; <i>Rhysopus</i> ; <i>Hexatrachus</i> ; common ancestor of <i>Pseudodichirus</i> and <i>Gynandrotarsus</i> ; either in an ancestor of <i>Dicheirus</i> and <i>Gynandromorphus</i> or independently in each genus
short hindtarsus	<i>Cenogmus</i> ; <i>Hypharpax</i> ; <i>Geopinus</i> ; <i>Anadaptus</i>
3 or more dorsal setigerous punctures on elytral interval III	<i>Gnathaphanus</i> ; <i>Diatypus</i> ; <i>Anisostichus</i> ; many species of <i>Pseudognathaphanus</i>
extra setae on abdominal sterna	common ancestor of <i>Triplosarus</i> , <i>Crasodactylus</i> , <i>Cenogmus</i> , and <i>Hypharpax</i> ; common ancestor of <i>Criniventer</i> and <i>Pseudanisotarsus</i> ; ancestor of <i>tucumana</i> lineage within <i>Anisotarsus</i> ; <i>Hexatrachus</i> ; some species of subgenus <i>Anisodactylus</i> ; some species of <i>Anadaptus</i> ; <i>Spongopus</i>
apical segment of stylus elongate	<i>Progonochaetus</i> ; <i>Geopinus</i>

Table 4. Plesiomorphic and apomorphic character states used in Fig. 242.

No.	Character	Character State	
		Plesiomorphic	Apomorphic
1	<b>Microsculpture</b> of elytron	isodiametric mesh	obsolete medially in ♂
2	<b>Head</b> eye	normal	reduced in most specimens
3	gena	wide	narrow
4	mental tooth	present and of moderate size	absent or vestigial
5	ligula apex	narrow	moderately to strongly expanded laterally in most specimens
6	<b>Pronotum</b> posterior angle	slightly acute to slightly obtuse	moderately to strongly rounded
7	side	slightly to moderately curved towards posterior angle	rectilinear or sinuate before posterior angle
8	lateral bead	normal	very prominent
9	<b>Legs</b> no. setae on posterior margin of hind-femur	2 to 6	10 to 12
10	<b>Elytron</b> distal setae on intervals III, V, VII	absent	present
11	<b>Hind wing</b> state	full	vestigial or dimorphic
12	<b>Abdomen</b> extra setae on sterna IV and V	absent	present

Table 4. Plesiomorphic and apomorphic character states used in Fig. 242 (concluded).

No.	Character	Character State	
		Plesiomorphic	Apomorphic
13	no. setae on sternum VI of ♂	2	4
14	<b>Male genitalia</b> median lobe	symmetrical	asymmetrical
15	large spine on internal sac	present	absent

Table 5. Plesiomorphic and apomorphic character states used in Fig. 243.

No.	Character	Character State	
		Plesiomorphic	Apomorphic
1	<b>Color</b> green tinge on dorsum	absent	present in most specimens
2	<b>Microsculpture</b> of frons	isodiametric mesh	small punctures
3	<b>Head</b> clypeo-ocular prolongation	present	absent
4	raised transverse ridge behind clypeal apex	present	absent
5	<b>Pronotum</b> shape	at most slightly widened basally	moderately widened basally (a) prominently widened basally
6	posterior angle	slightly obtuse to slightly acute	broadly rounded
7	lateral bead	complete and moderately prominent	obsolescent anteriorly (a) very prominent and thick
8	<b>Legs</b> first segment of protarsus of ♀	not expanded laterally	slightly to moderately expanded laterally (a) strongly expanded laterally
9	<b>Elytron</b> humeral tooth	absent	present
10	subapical sinuation	obsolescent	moderately prominent
11	<b>Abdomen</b> no. of ambulatory setae on sternum VI of ♂	4	2 (4 in occasional specimens of <i>haplomus</i> )

Table 5. Plesiomorphic and apomorphic character states used in Fig. 243. (concluded).

No.	Character	Character State	
		Plesiomorphic	Apomorphic
	<b>Male Genitalia</b>		
12	apical disc on median lobe	present	absent
13	arrangement of inverted internal sac inside median lobe	following shape of median lobe	irregularly coiled

Table 6. Distribution by numbers of species of the groups of Anisodactylina in the major faunal regions. (introduced species recorded only by their place of origin).

Taxa	Nearctic	Neotropical	Palaearctic	Ethiopian	Oriental	Australian	Nearctic + Neotropical	Palaearctic + Oriental	Oriental + Australian	Oriental + Palaearctic + Ethiopian
<i>Allocinopus</i>						5				
<i>Triplosarus</i>						2				
<i>Crasodactylus</i>					1					1
<i>Cenogmus</i>						3				
<i>Hypharpax</i>					1	27			2	
<i>Gnathaphanus</i> (1 in Polynesia)					5	17			2	
<i>Pseudanisotarsus</i>		1								
<i>Criniventer</i>		1								
<i>Anisotarsus</i>	11	12				30	2			
<i>Notiobia</i>		27								
<i>Diatypus</i>				10						
<i>Anisostichus</i>		4								
<i>Scybalicus</i>			3							
<i>Progonochaetus</i>				37	1					
<i>Eudichirus</i>				3						
<i>Phanagnathus</i>				1						
<i>Pseudognathaphanus</i>				2	6					
<i>Chydaeus</i>			5		14	1		2		
<i>Harpalomimetes</i>					1			1		



Table 6. Distribution by numbers of species of the groups of Anisodactylina in the major faunal regions. (introduced species recorded only by their place of origin). (continued).

Taxa	Nearctic	Neotropical	Palaearctic	Ethiopian	Oriental	Australian	Nearctic + Neotropical	Palaearctic + Oriental	Oriental + Australian	Oriental + Palaearctic + Ethiopian
<i>Rhysopus</i>					1					
<i>Xestonotus</i>	1									
<i>Anisodactylus</i>	12		11		1					
<i>Pseudanisodactylus</i>			2							
<i>Pseudhexatrachus</i>			2							
<i>Hexatrachus</i>			3							
<i>Pseudodichirus</i>			1							
<i>Gynandrotarsus</i>	10									
<i>Anadaptus</i>	8									
<i>Spongopus</i>	1									
<i>Aplocentrus</i>	2									
<i>Pseudaplocentrus</i>	1									
<i>Geopinus</i>	1									
<i>Pseudamphasia</i>	1									
<i>Amphasia</i>	1									
<i>Gynandromorphus</i>			1							
<i>Diachromus</i>			1							
<i>Dicheirus</i>	5									
Total endemic species	54	45	29	53	31	85				1

Table 6. Distribution by number of species of the groups of Anisodactylina in the major faunal regions. (introduced species recorded only by their place of origin). (concluded).

Taxa	Nearctic	Neotropical	Palaearctic	Ethiopian	Oriental	Australian	Nearctic + Neotropical	Palaearctic + Oriental	Oriental + Australian	Oriental + Palaearctic + Ethiopian
Total number supra-specific taxa	12	5	9	7	9	7				1
Average number of endemic species per supra-specific taxon	4.5	9	3.6	7.6	3.4	12.1				1
Number of endemic supra-specific taxa	10	4	6	3	1	3				
% endemic supra-specific taxa	83	80	67	43	11	43				
Total no. spp. (includes non endemics)	56	47	32	54	39	89				
Total no. spp./taxon	4.7	9.4	3.5	7.7	4.3	12.7				

Table 7. Distribution of the genera and subgenera of the subtribe Anisodactylinae in temperate and tropical regions.

Taxa	Temperate	Tropical
<i>Allocinopus</i>	x	
<i>Triplosarus</i>	x	
<i>Crasodactylus</i>	x	x
<i>Cenogmus</i>	x	
<i>Hypharpax</i>	x	x
<i>Gnathaphanus</i>	x	
<i>Pseudanisotarsus</i>	x	
<i>Criniventer</i>	x	
<i>Anisotarsus</i>	x	
<i>Notiobia</i>		x
<i>Diatypus</i>		x
<i>Anisostichus</i>	x	
<i>Scybalicus</i>	x	
<i>Progonochaetus</i>		x
<i>Eudichirus</i>		x
<i>Phanagnathus</i>		x
<i>Pseudognathaphanus</i>		x
<i>Chydaeus</i>	x	
<i>Harpalomimetes</i>	x	x
<i>Rhysopus</i>		x
<i>Xestonotus</i>	x	
<i>Anisodactylus</i>	x	x (1 or 2 species only)

Table 7. Distribution of the genera and subgenera of the subtribe Anisodactylina in temperate and tropical regions. (concluded).

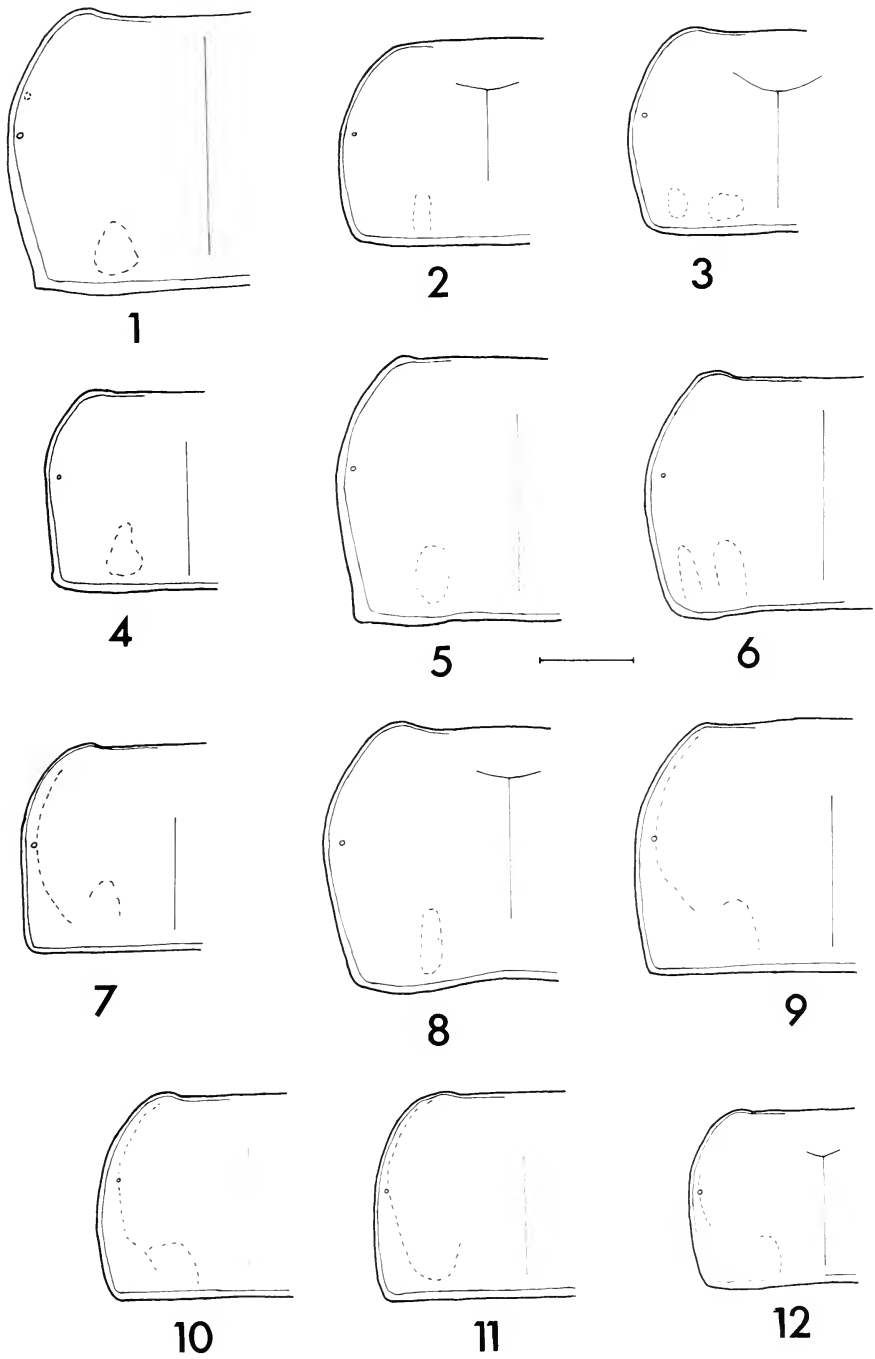
Taxa	Temperate	Tropical
<i>Pseudanisodactylus</i>	x	
<i>Pseudhexatrachus</i>	x	
<i>Hexatrachus</i>	x	
<i>Pseudodichirus</i>	x	
<i>Gynandrotarsus</i>	x	
<i>Anadaptus</i>	x	
<i>Spongopus</i>	x	
<i>Aplocentrus</i>	x	
<i>Pseudaplocentrus</i>	x	
<i>Geopinus</i>	x	
<i>Pseudamphasia</i>	x	
<i>Amphasia</i>	x	
<i>Gynandromorphus</i>	x	
<i>Diachromus</i>	x	
<i>Dicheirus</i>	x	
TOTAL	30	11
ENDEMICS	26	7

Table 8. Range extents of species of *Anisotarsus*.

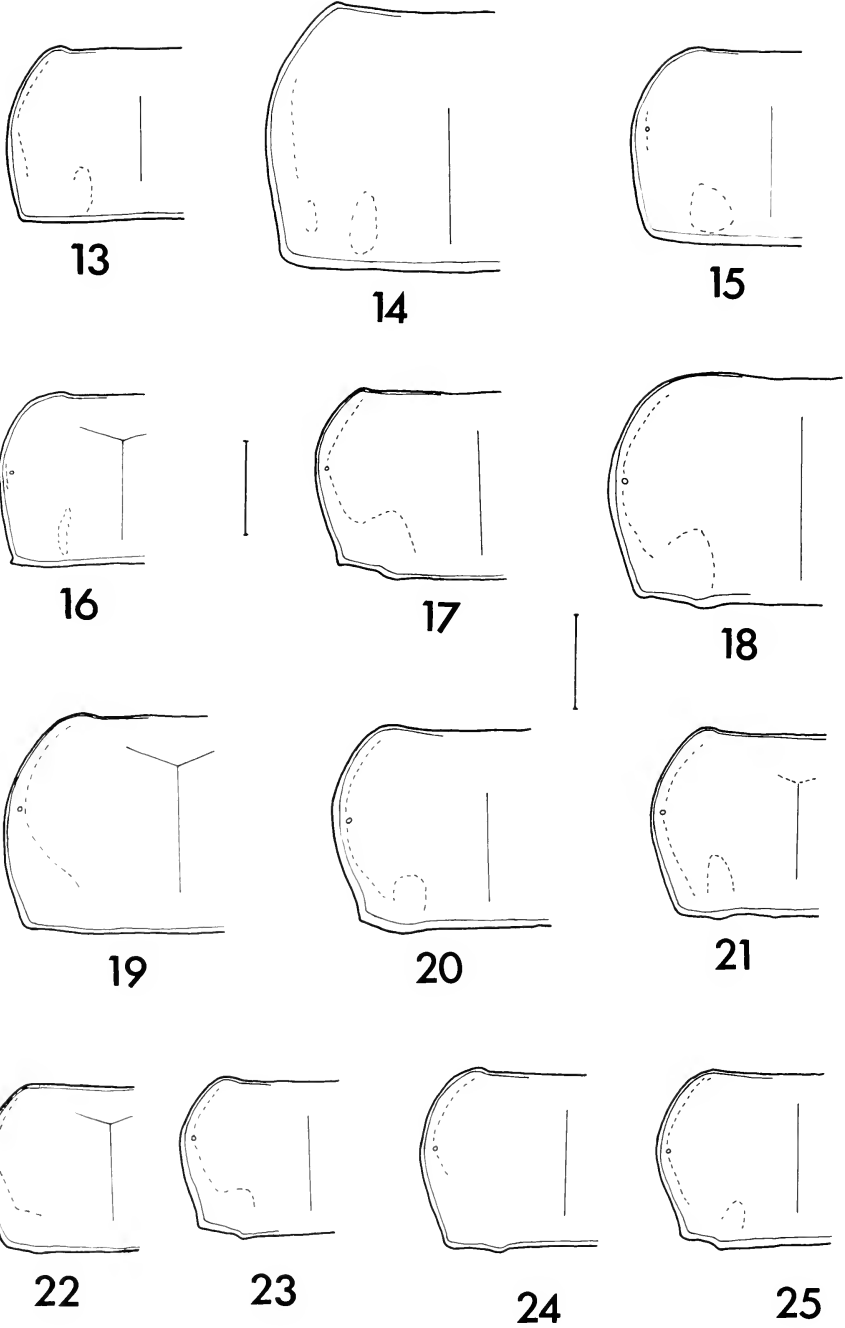
SPECIES	MAXIMUM RANGE EXTENT
Distance Range (in miles)	(in miles)
0-500	
<i>hilariola</i>	under 100
<i>lamprota</i>	150
<i>schlingeri</i>	375
<i>cyanippa</i>	425
501-1000	
<i>maculicornis</i>	725
<i>virescens</i>	750
<i>flebilis</i>	900
1001-2000	
<i>brevicollis</i>	1500
<i>purpurascens</i>	1650
<i>picea</i>	1750
<i>nitidipennis</i>	1850
2001-2950	
<i>mexicana</i>	2350
<i>terminata</i>	2950

Table 9. Range extents of species of *Gynandrotarsus*.

SPECIES	MAXIMUM RANGE EXTENT
Distance Range	
(in miles)	(in miles)
0-500	
none	
501-1000	
<i>harpaloides</i>	650
<i>darlingtoni</i>	850
<i>opaculus</i>	1000
1001-1500	
<i>texanus</i>	1250
<i>haplomus</i>	1400
<i>ovularis</i>	1500
<i>dulcicollis</i>	1500
1501-2000	
<i>anthracinus</i>	1650
<i>merula</i>	1900
2001-2250	
<i>rusticus</i>	2250

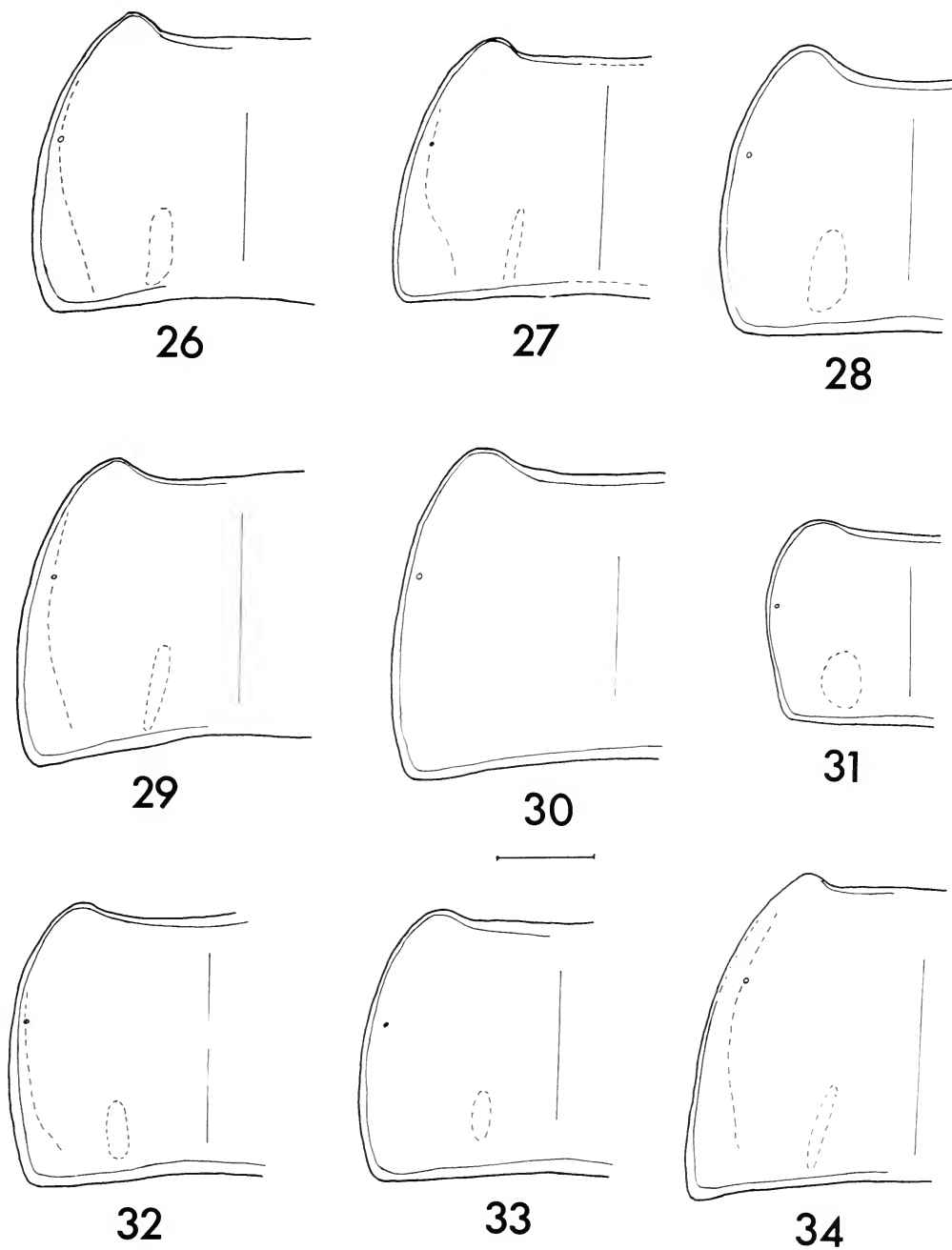


Figs. 1-12. Pronota of species of the subgenus *Anisotarsus*. 1. *lamprota*. 2. *virescens*. 3. *purpurascens*. 4. *schlingeri*. 5. *mexicana*. 6. *cyanippa*. 7. *picea*. 8. *hilariola*. 9. *maculicornis*. 10. *terminata* (Chicago, Illinois). 11. *terminata* (Texas). 12. *terminata* (Florida). (scale lines 1 mm.)

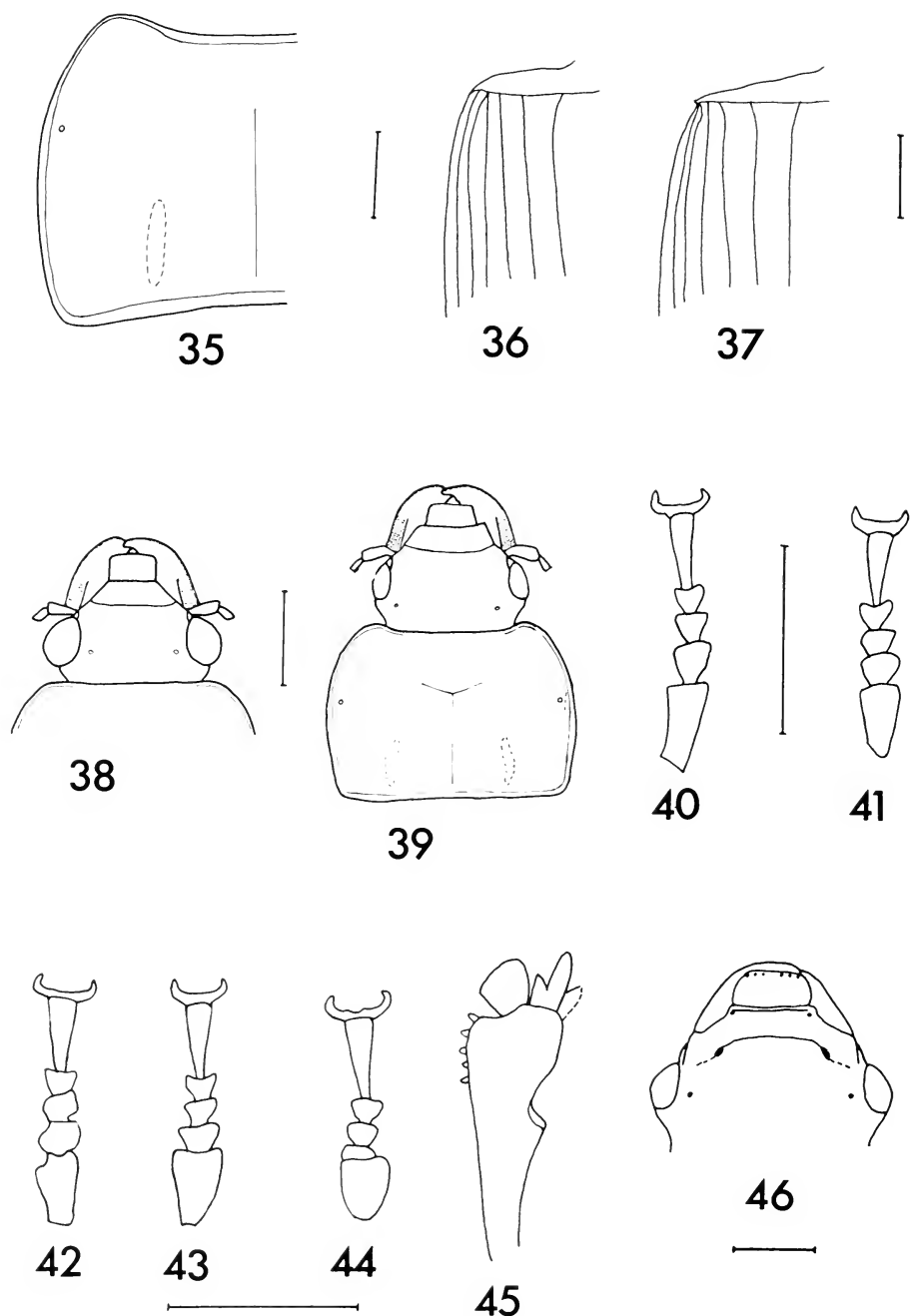


Figs. 13-16. Pronota of species of the subgenus *Anisotarsus*. 13. *terminata* (Mexico). 14. *brevicollis*. 15. *flebilis*. 16. *niti-dipennis*. Figs. 17-25. Pronota of species of the subgenus *Notiobia*. 17. *limbipennis*. 18. *leiroides*. 19. *cooperi*. 20. *melaena*. 21. *pallipes*. 22. *ewarti*. 23. *umbrifera*. 24. *obscura*. 25. *umbrata*. (scale lines 1 mm).

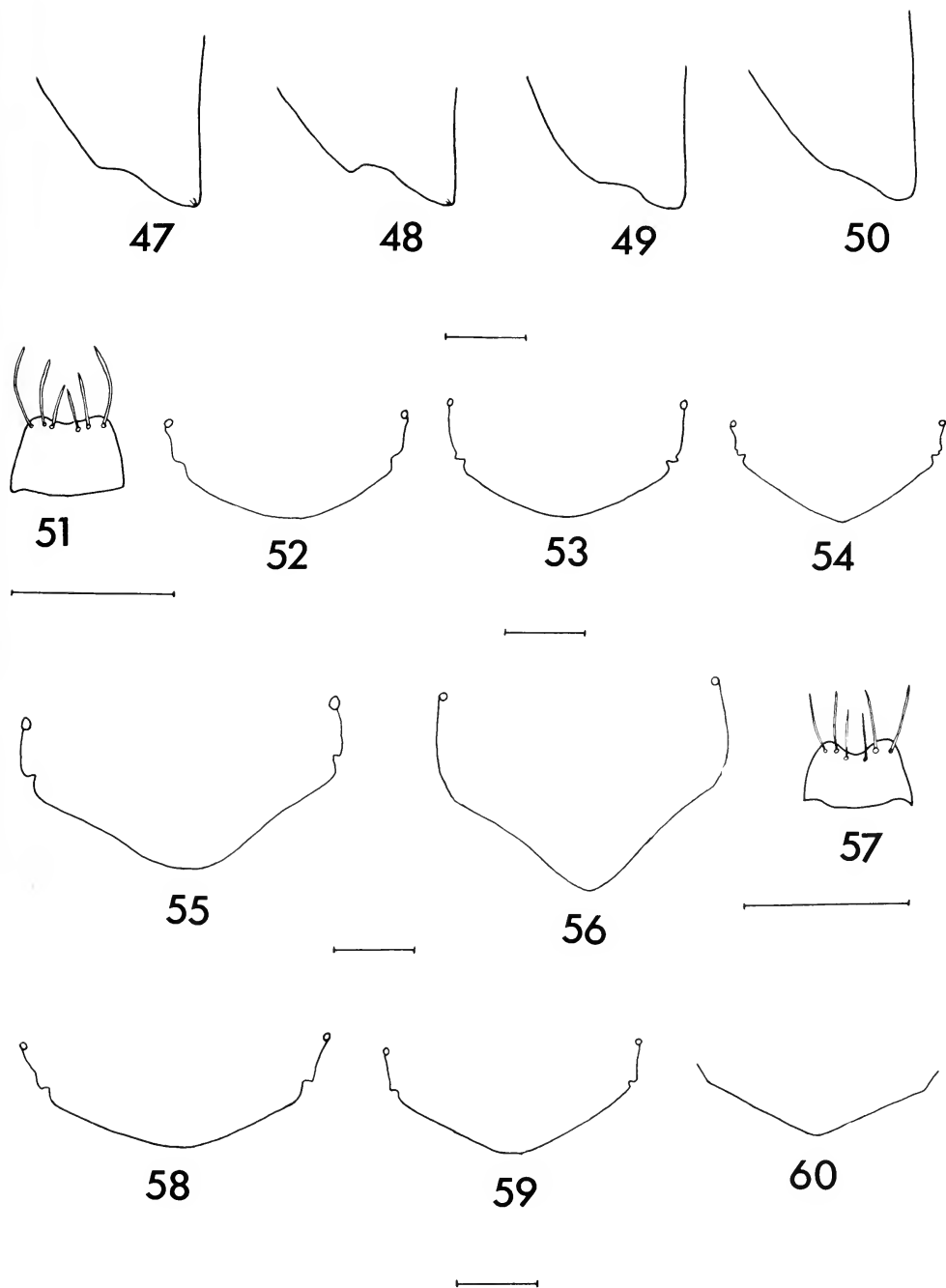




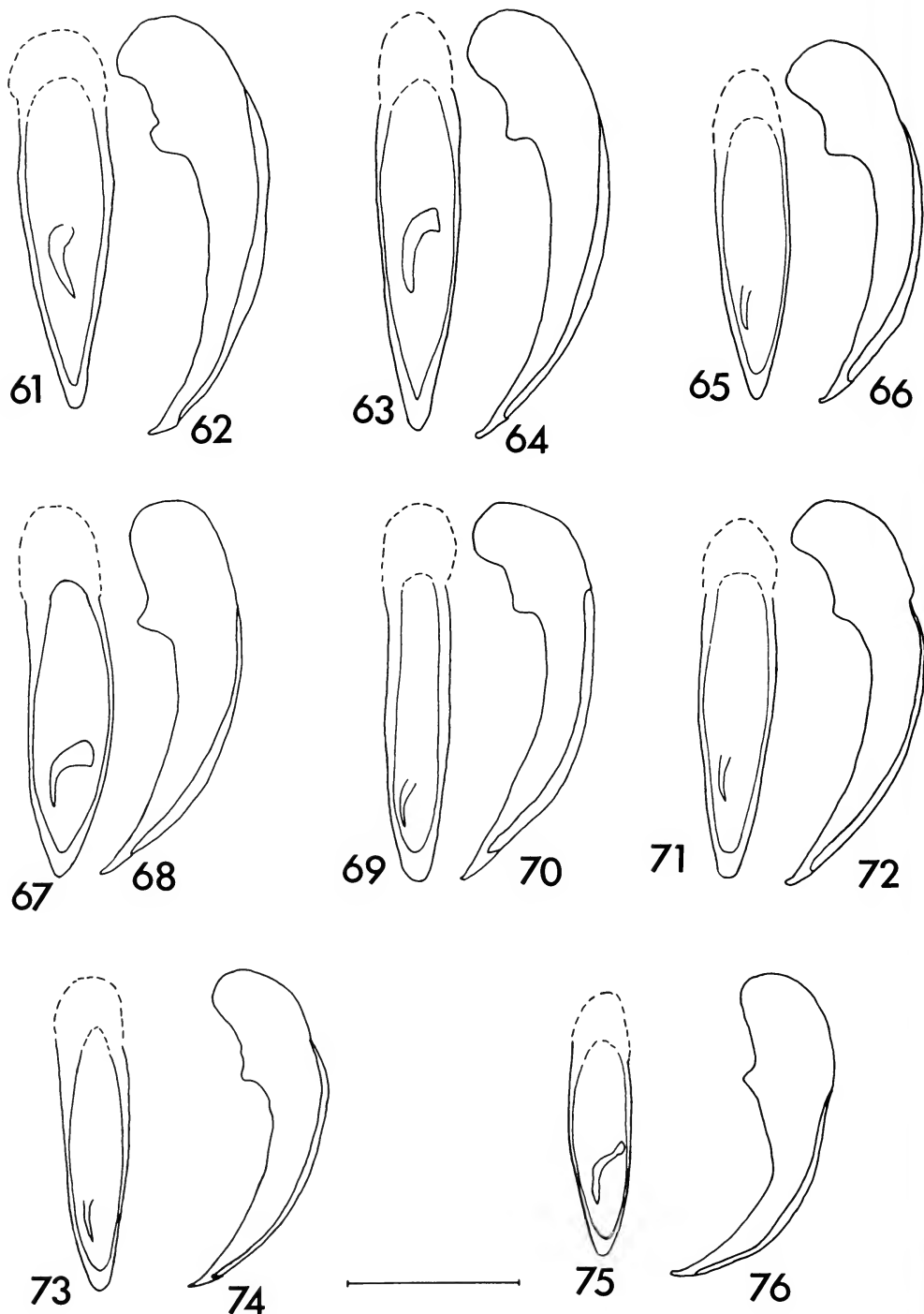
Figs. 26-34. Pronota of species of the subgenus *Gynandrotarsus*. 26. *ovularis*. 27. *rusticus*. 28. *dulcicollis*. 29. *merula*. 30. *anthracinus*. 31. *harpaloides*. 32. *texanus*. 33. *opaculus*. 34. *haplomus*. (scale line 1 mm).



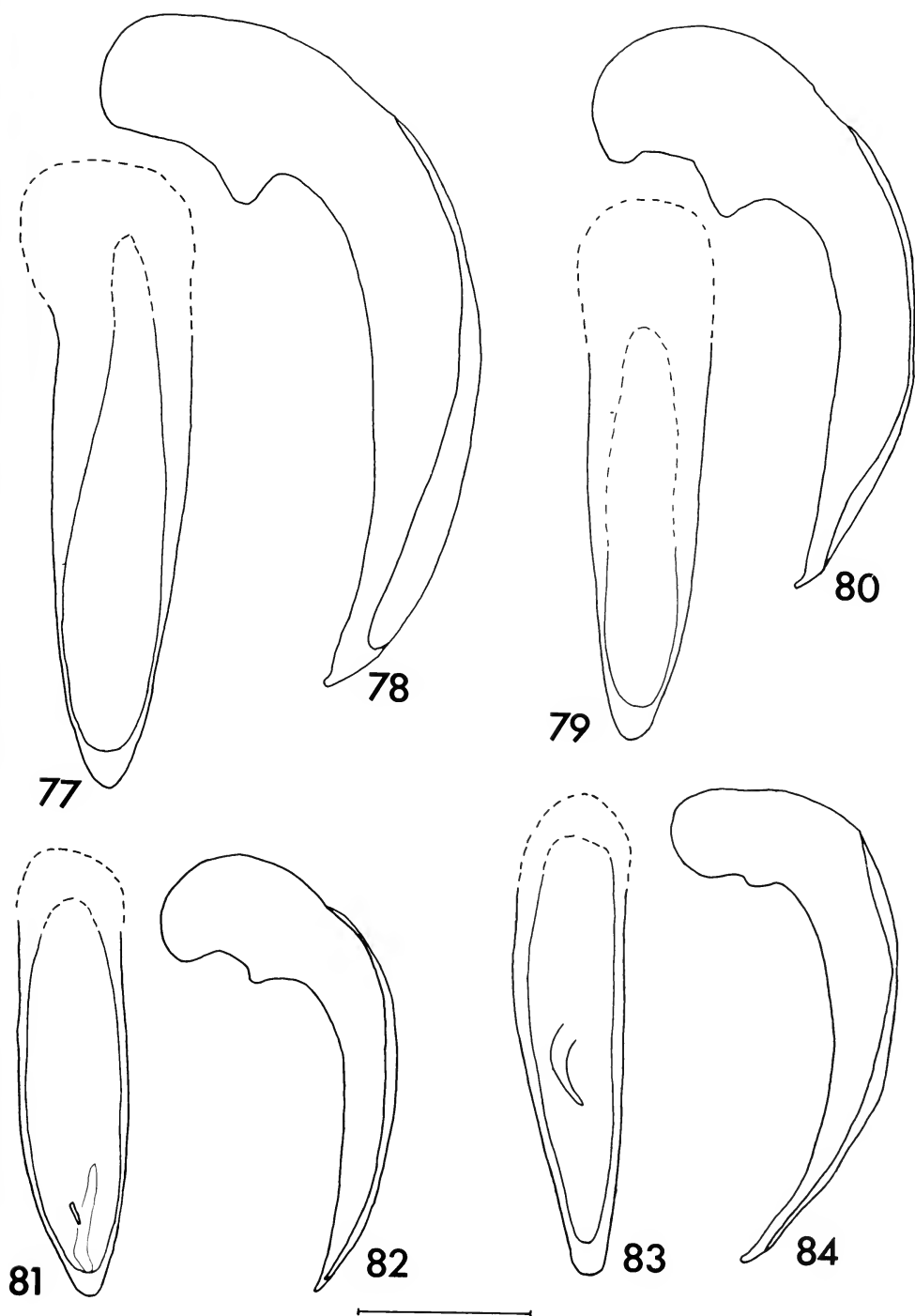
Figs. 35-37. Body parts of species of the subgenus *Gynandrotarsus*. 35. Pronotum of *darlingtoni*. 36. Humerus of *darlingtoni*. 37. Humerus of *anthracinus*. Figs. 38-39. Body parts of species of the subgenus *Anisotarsus*. 38. Head of *terminata*. 39. Head and pronotum of *nitidipennis*. Figs. 40-44. Venter of foretarsi of females of species of the subgenus *Gynandrotarsus* (setae and spines omitted). 40. *rusticus*. 41. *dulcicollis*. 42. *texanus*. 43. *opaculus*. 44. *harpaloides*. Figs. 45-46. Body parts of species of subgenus *Gynandrotarsus*. 45. Protibia and apical spur of *dulcicollis*. 46. Head of *opaculus* with clypeo-ocular prolongations indicated as dashed lines. (scale lines 1 mm).



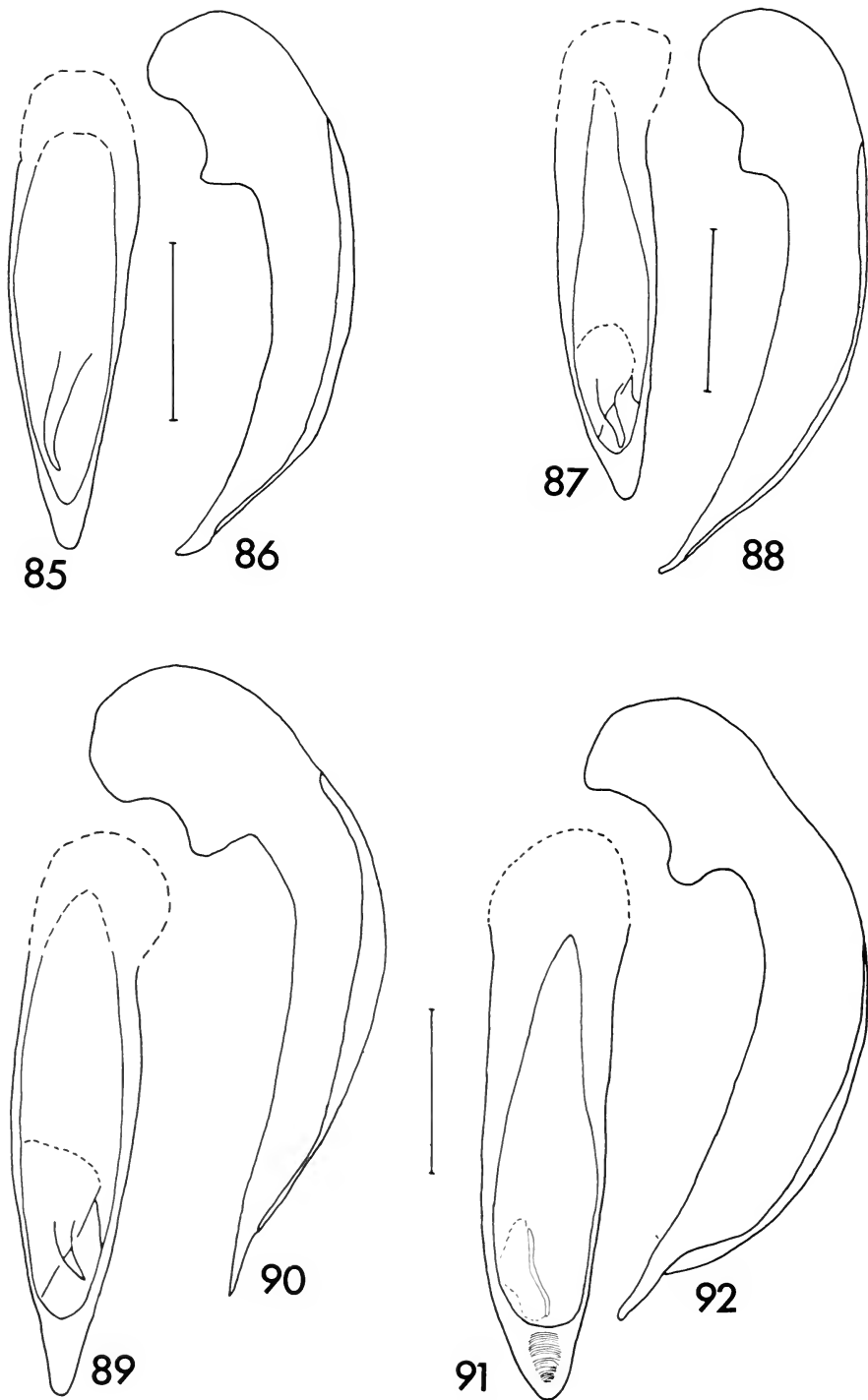
Figs. 47-50. Elytral apices of species of the subgenus *Notiobia*. 47. *limbipennis* (Mexico). 48. *limbipennis* (Panama). 49. *umbrata*. 50. *obscura*. Fig. 51. Labrum of *Notiobia (N.) obscura*. Figs. 52-56. Apex of abdominal tergum VIII of females of the subgenus *Notiobia*. 52. *pallipes*. 53. *umbrata*. 54. *umbrifera*. 55. *leiroides*. 56. *limbipennis*. Fig. 57. Labrum of *Notiobia (N.) ewarti*. Figs. 58-59. Apex of abdominal tergum VIII of females of the subgenus *Notiobia*. 58. *cooperi*. 59. *melaena*. Fig. 60. Apex of abdominal tergum VIII of female of *Anisodactylus (Gynandrotarsus) dulcicollis*. (scale lines 1 mm).



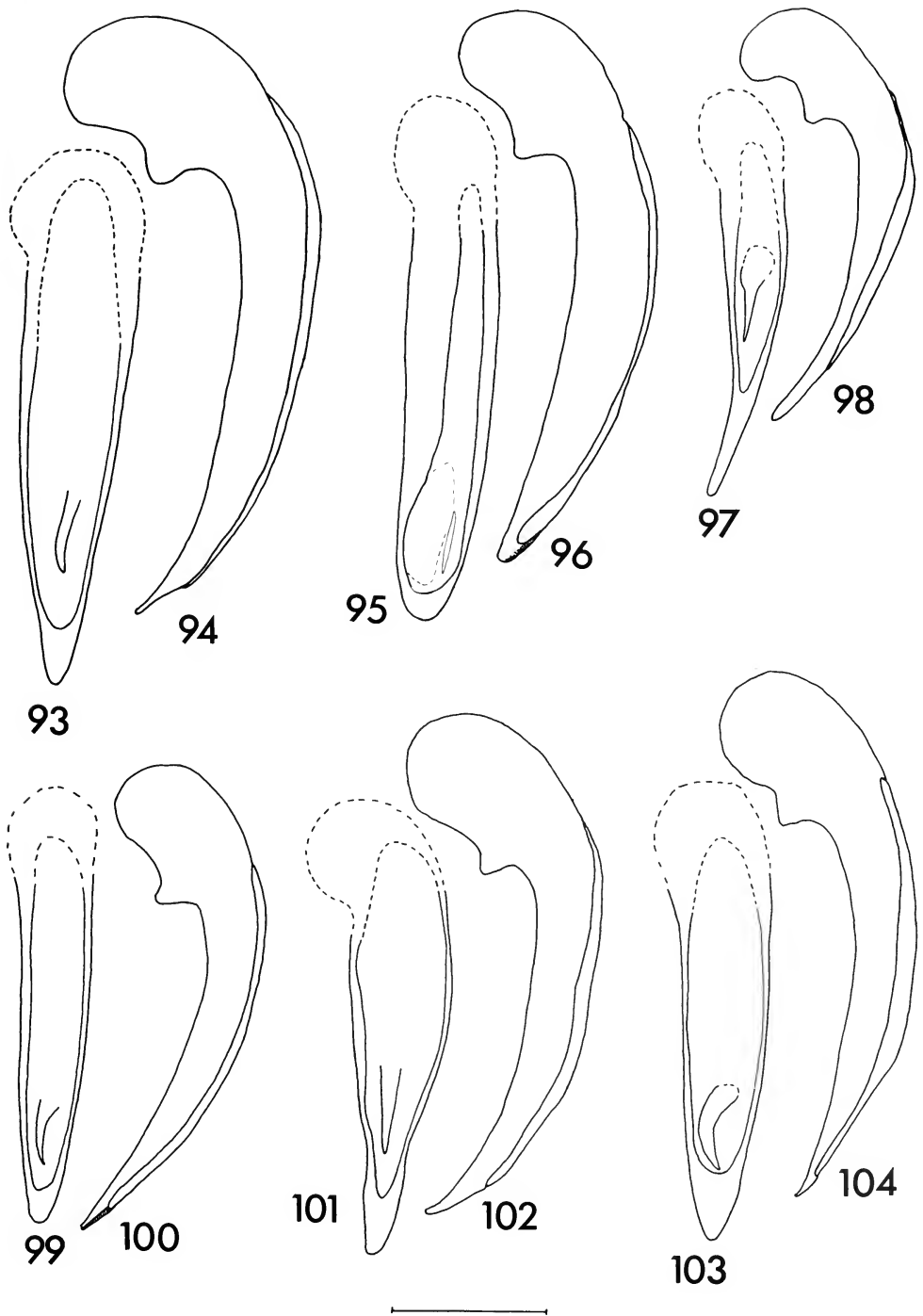
Figs. 61-76. Median lobes of male genitalia of species of the subgenus *Anisotarsus*. 61 & 62. Dorsal and lateral aspect of northern morph of *terminata*. 63 & 64. Dorsal and lateral aspect of *terminata* (Mexico, Nuevo Leon, 20.3 mi. N. Sabinas Hidalgo). 65 & 66. Dorsal and lateral aspect of *terminata* (Mexico, Hidalgo, 7.2 mi. S. Zimapan). 67 & 68. Dorsal and lateral aspect of *purpurascens*. 69 & 70. Dorsal and lateral aspect of *virescens*. 71 & 72. Dorsal and lateral aspect of *flebilis*. 73 & 74. Dorsal and lateral aspect of *nitidipennis*. 75 & 76. Dorsal and lateral aspect of *schlingerii*. (scale line 1 mm).



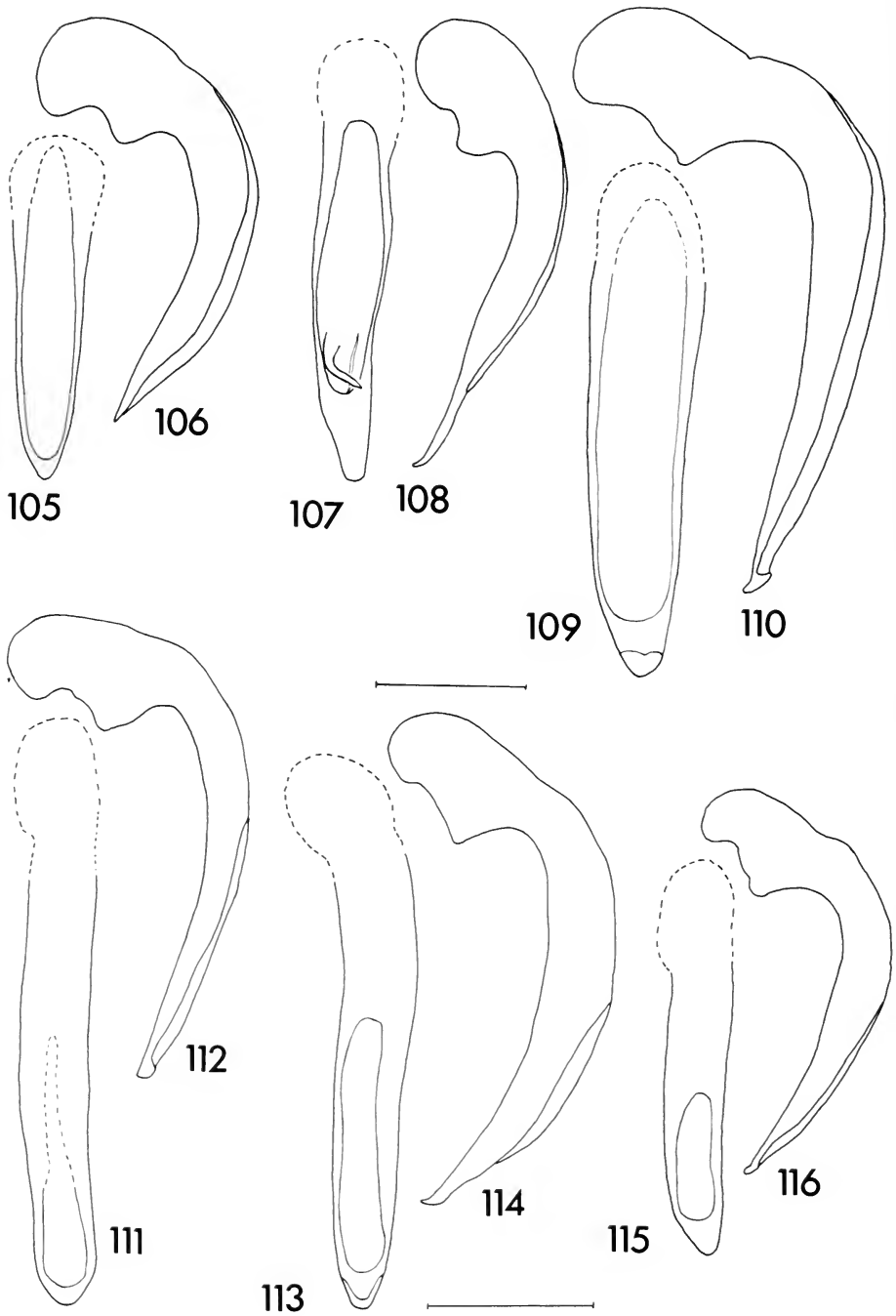
Figs. 77-84. Median lobes of male genitalia of species of the subgenus *Anisotarsus*. 77 & 78. Dorsal and lateral aspect of *lamprota*. 79 & 80. Dorsal and lateral aspect of *mexicana*. 81 & 82. Dorsal and lateral aspect of *picea*. 83 & 84. Dorsal and lateral aspect of *maculicornis*. (scale line 1 mm).



Figs. 85-90. Median lobes of male genitalia of species of the subgenus *Anisotarsus*. 85 & 86. Dorsal and lateral aspect of *brevicollis*. 87 & 88. Dorsal and lateral aspect of *cyanippra*. 89 & 90. Dorsal and lateral aspect of *hilariola*. Figs. 91 & 92. Dorsal and lateral aspect of median lobe of male genitalia of *Notiobia* (*N.*) *leiroides*. (scale lines 1 mm).

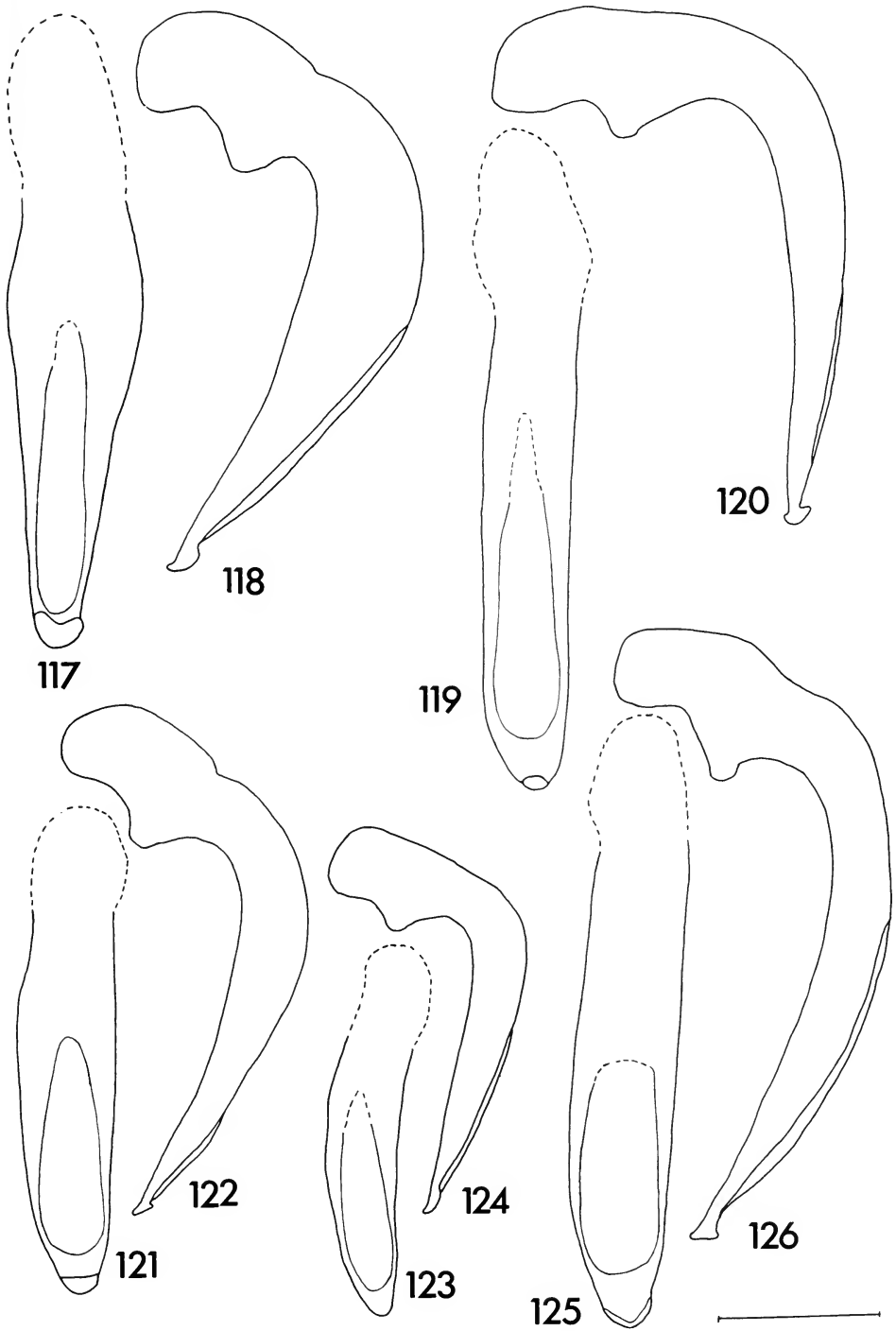


Figs. 93-104. Median lobes of male genitalia of species of the subgenus *Notiobia*. 93 & 94. Dorsal and lateral aspect of *melaena*. 95 & 96. Dorsal and lateral aspect of *limbipennis*. 97 & 98. Dorsal and lateral aspect of *umbrifera*. 99 & 100. Dorsal and lateral aspect of *obscura*. 101 & 102. Dorsal and lateral aspect of *pallipes*. 103 & 104. Dorsal and lateral aspect of *cooperi*. (scale line 1 mm).

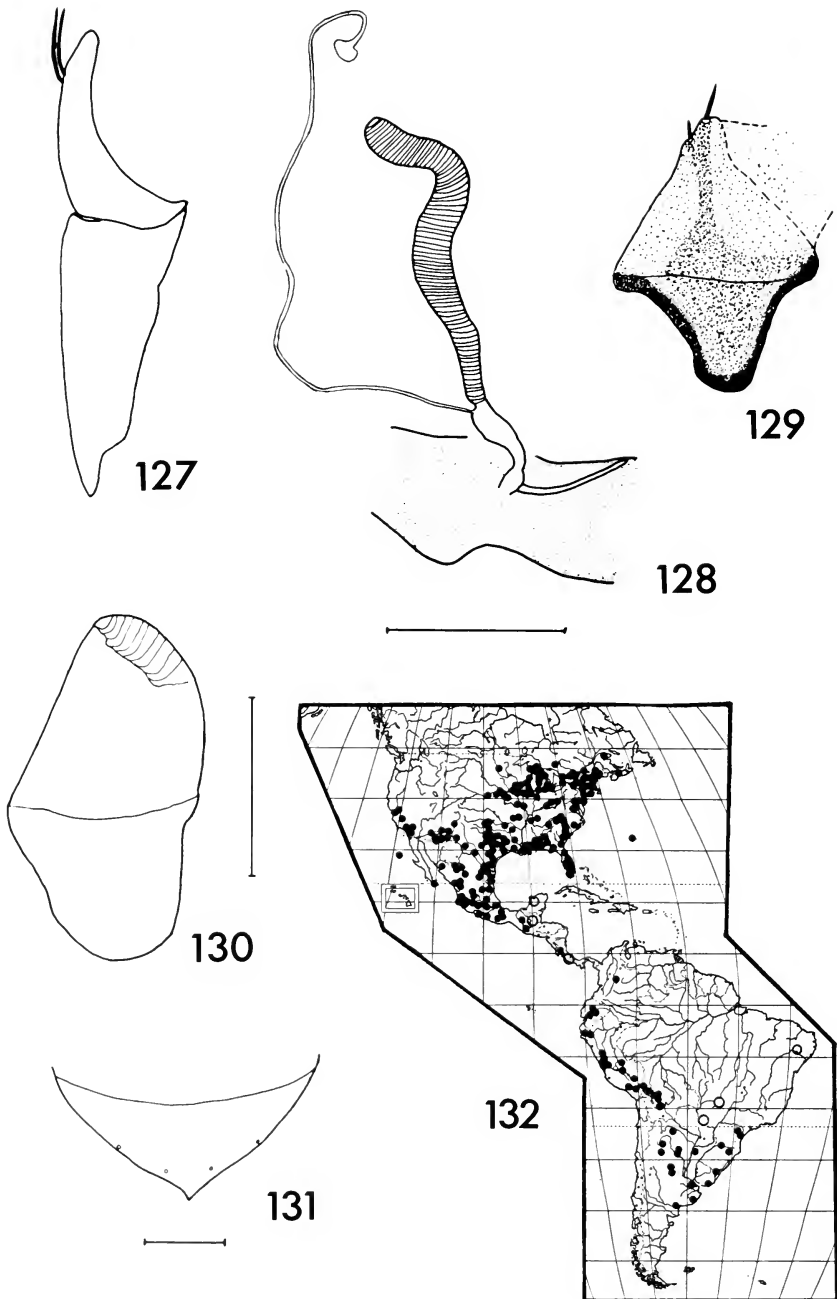


Figs. 105-108. Median lobes of male genitalia of species of the subgenus *Notiobia*. 105 & 106. Dorsal and lateral aspect of *umbrata*. 107 & 108. Dorsal and lateral aspect of *ewarti*. Figs. 109-116. Median lobes of male genitalia of species of the subgenus *Gynandrotarsus*. 109 & 110. Dorsal and lateral aspect of *darlingtoni*. 111 & 112. Dorsal and lateral aspect of *opaculus*. 113 & 114. Dorsal and lateral aspect of *haplomus*. 115 & 116. Dorsal and lateral aspect of *rusticus*. (scale lines 1 mm).

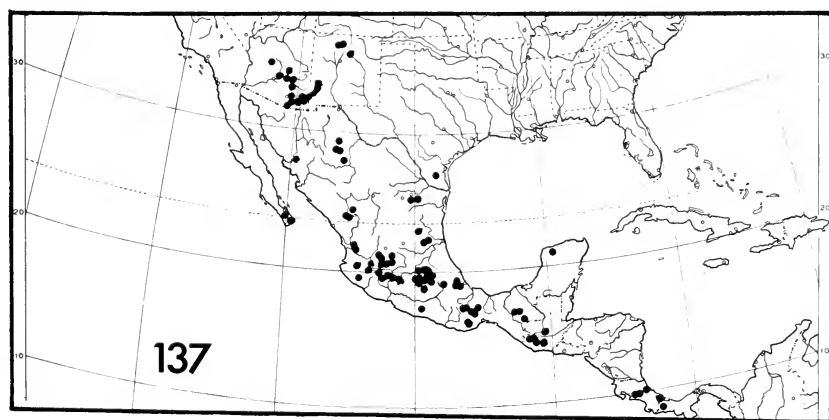
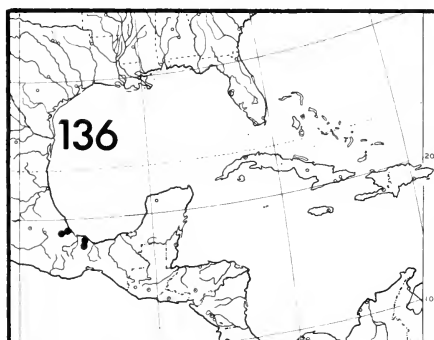
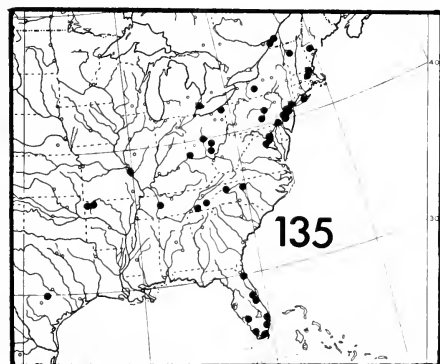
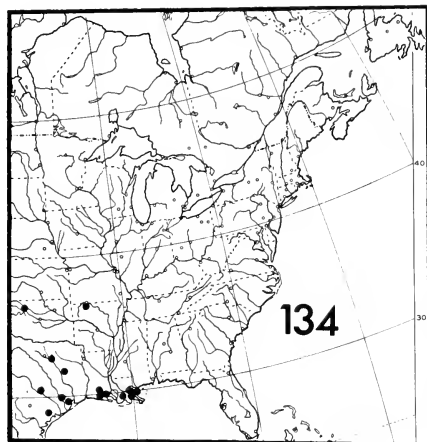
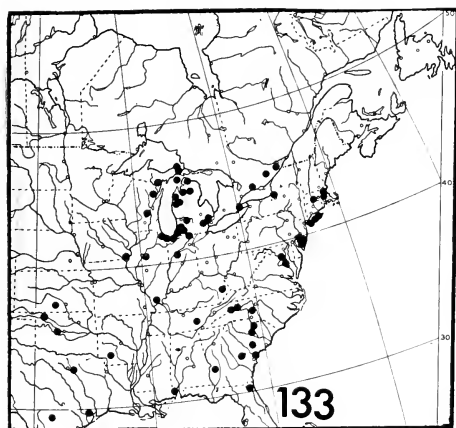




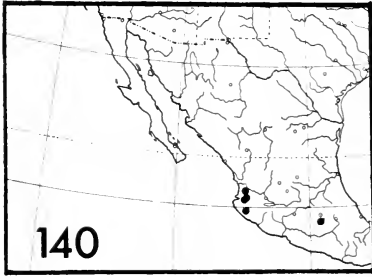
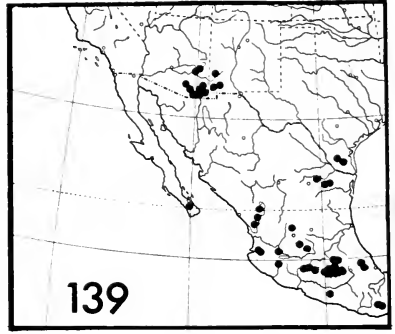
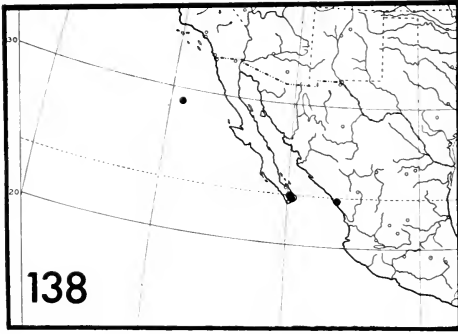
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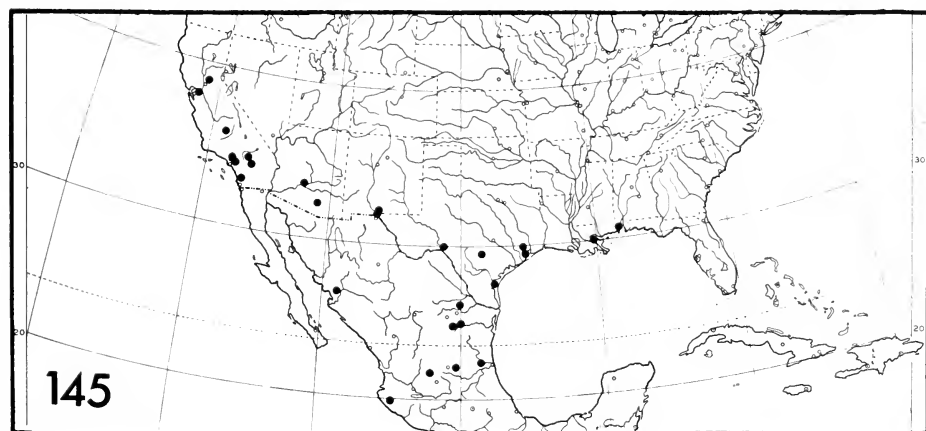
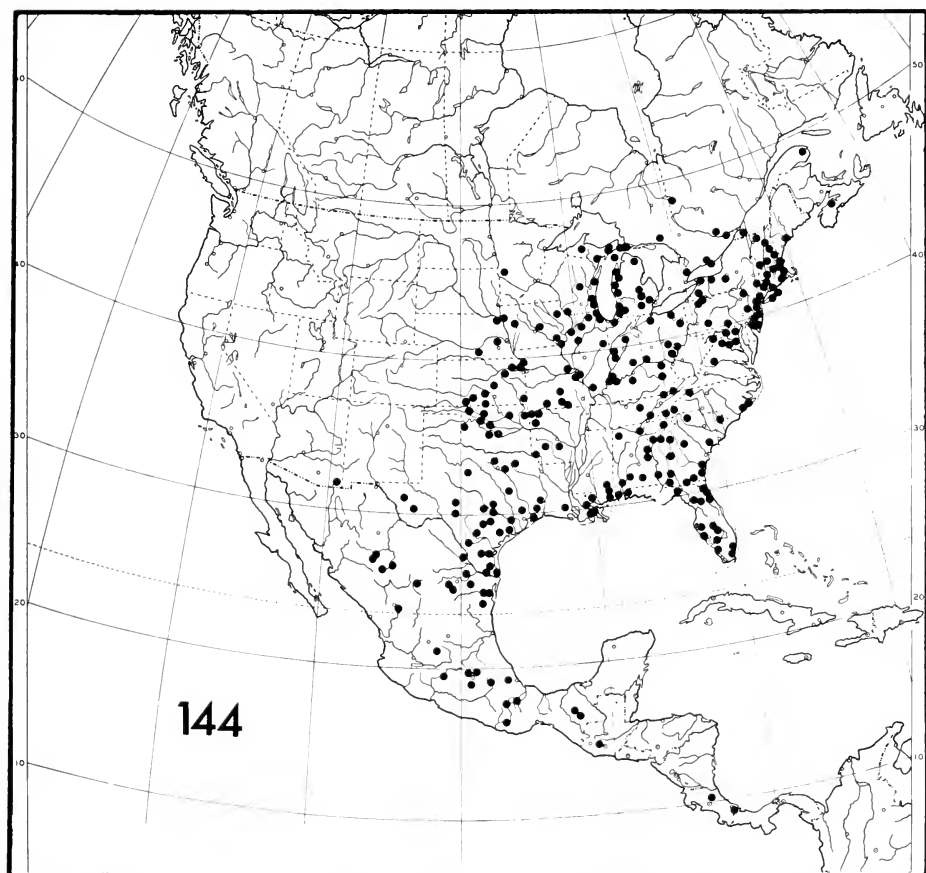
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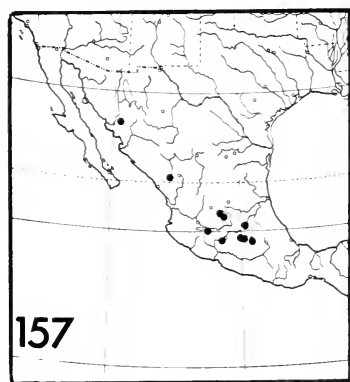
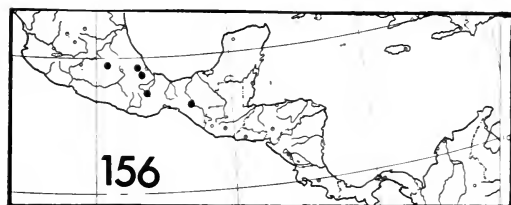
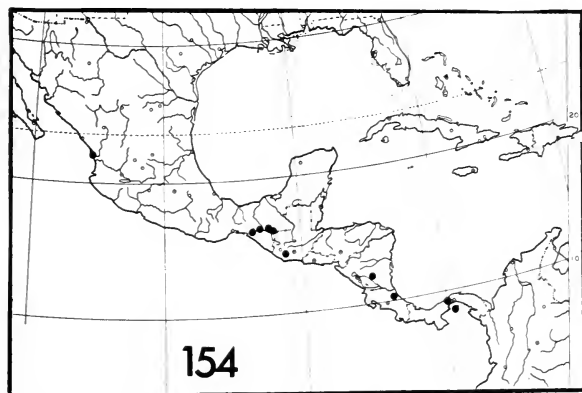
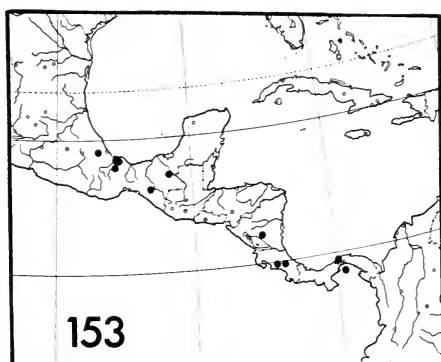
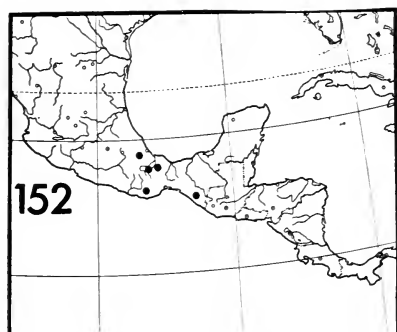
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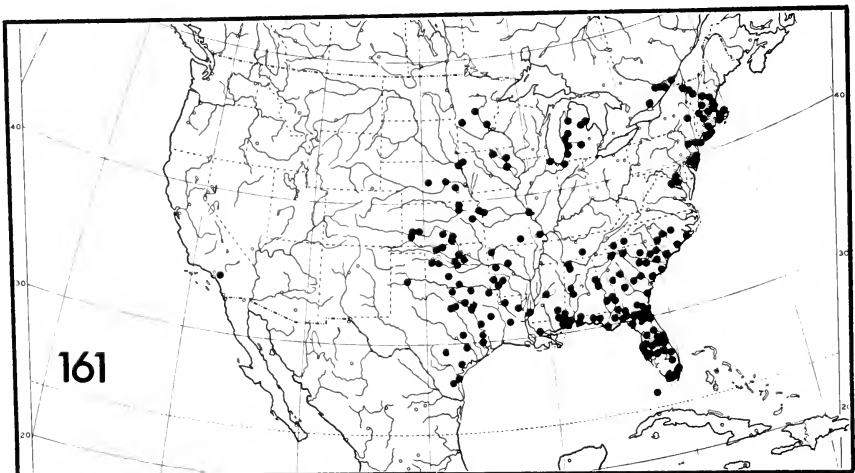
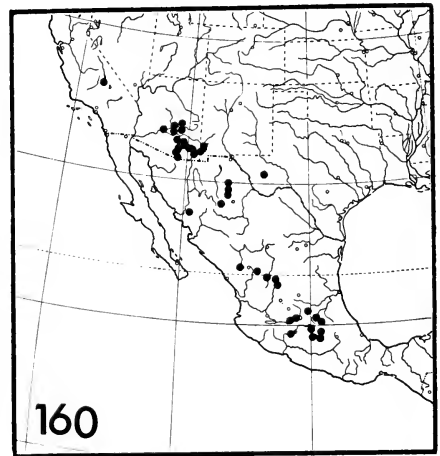
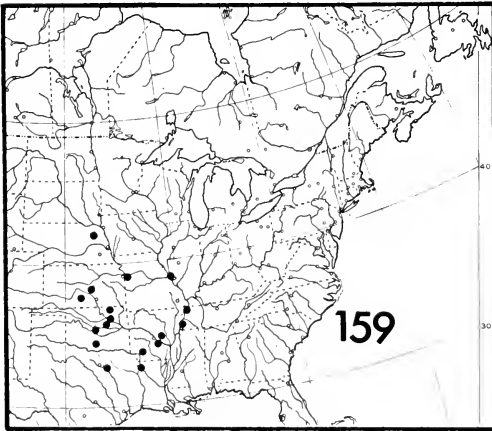
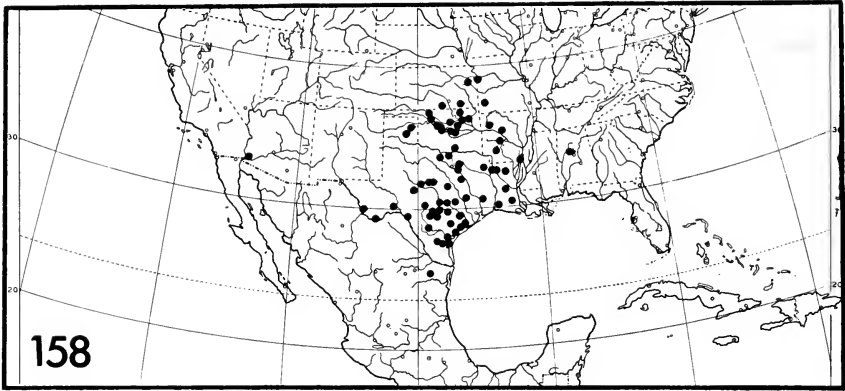
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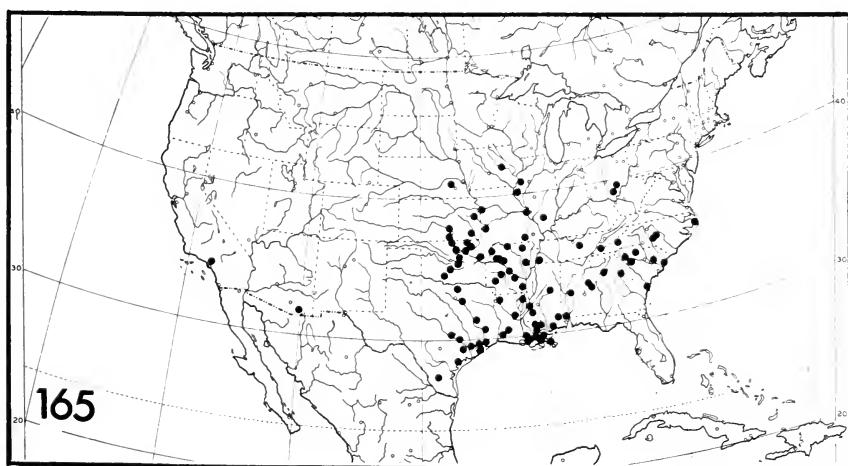
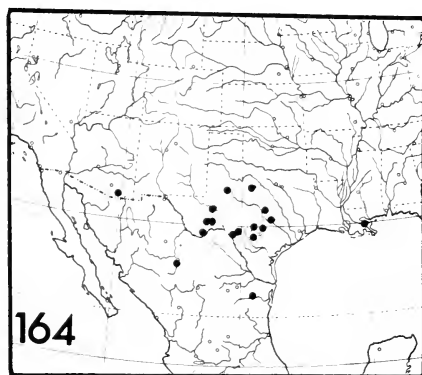
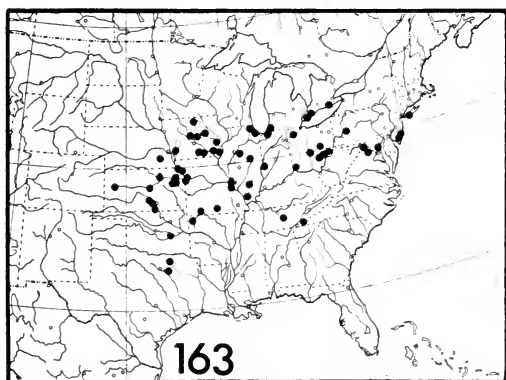
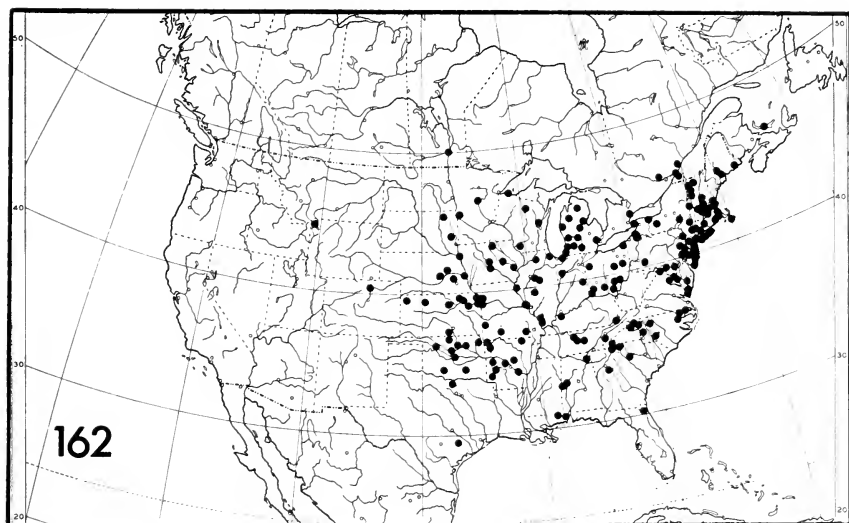


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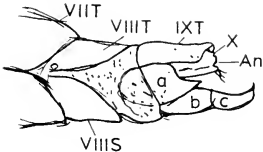
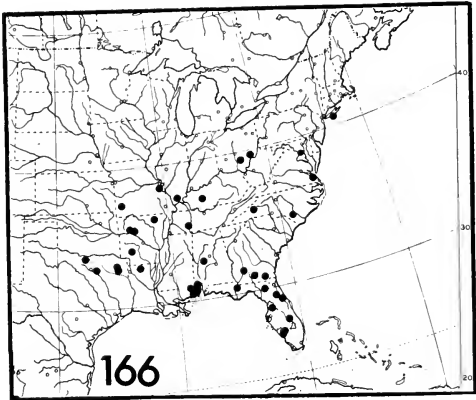


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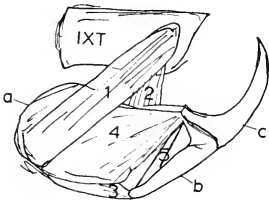




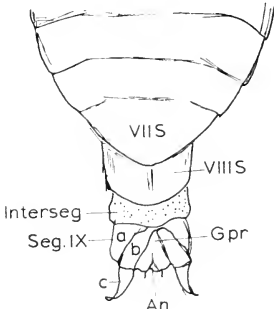
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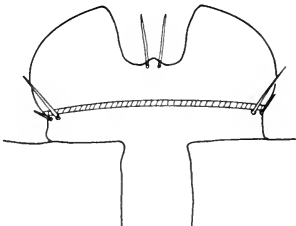
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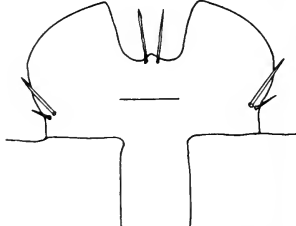
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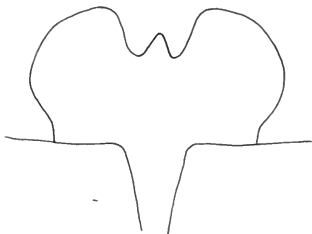
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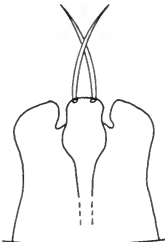
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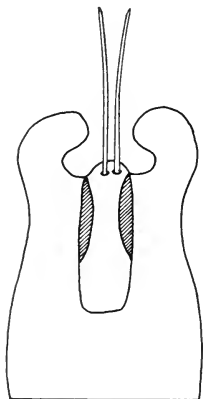
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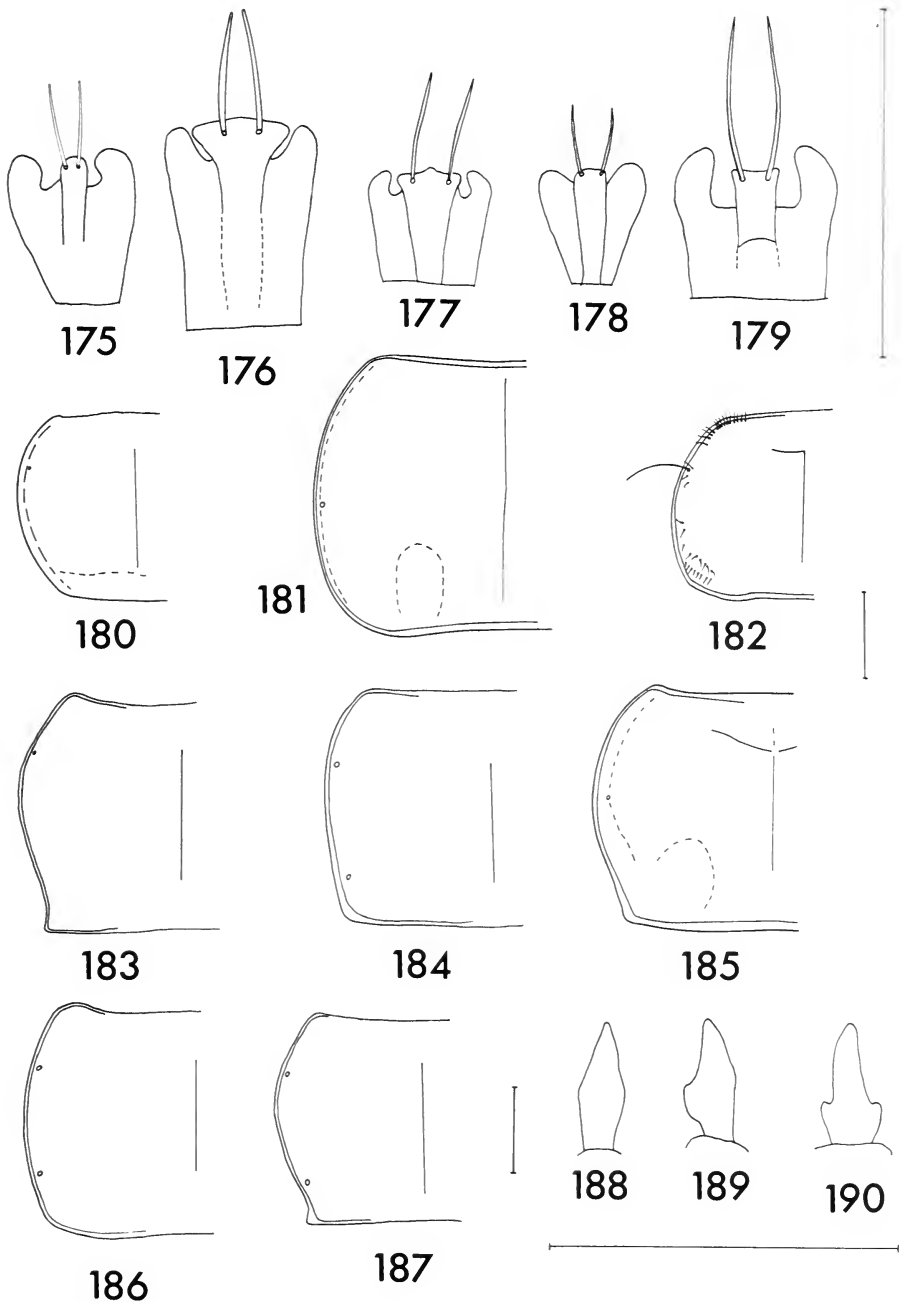


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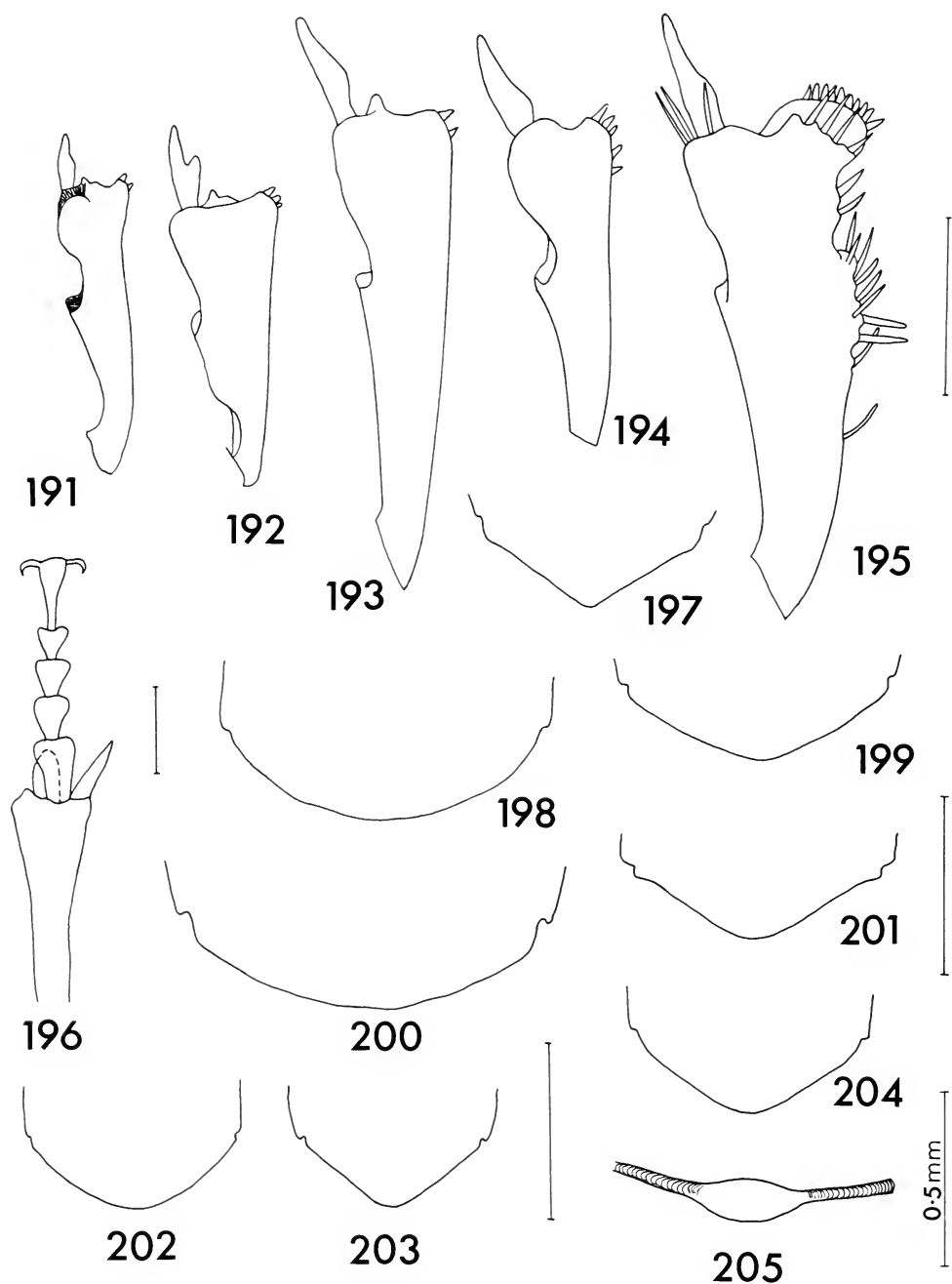
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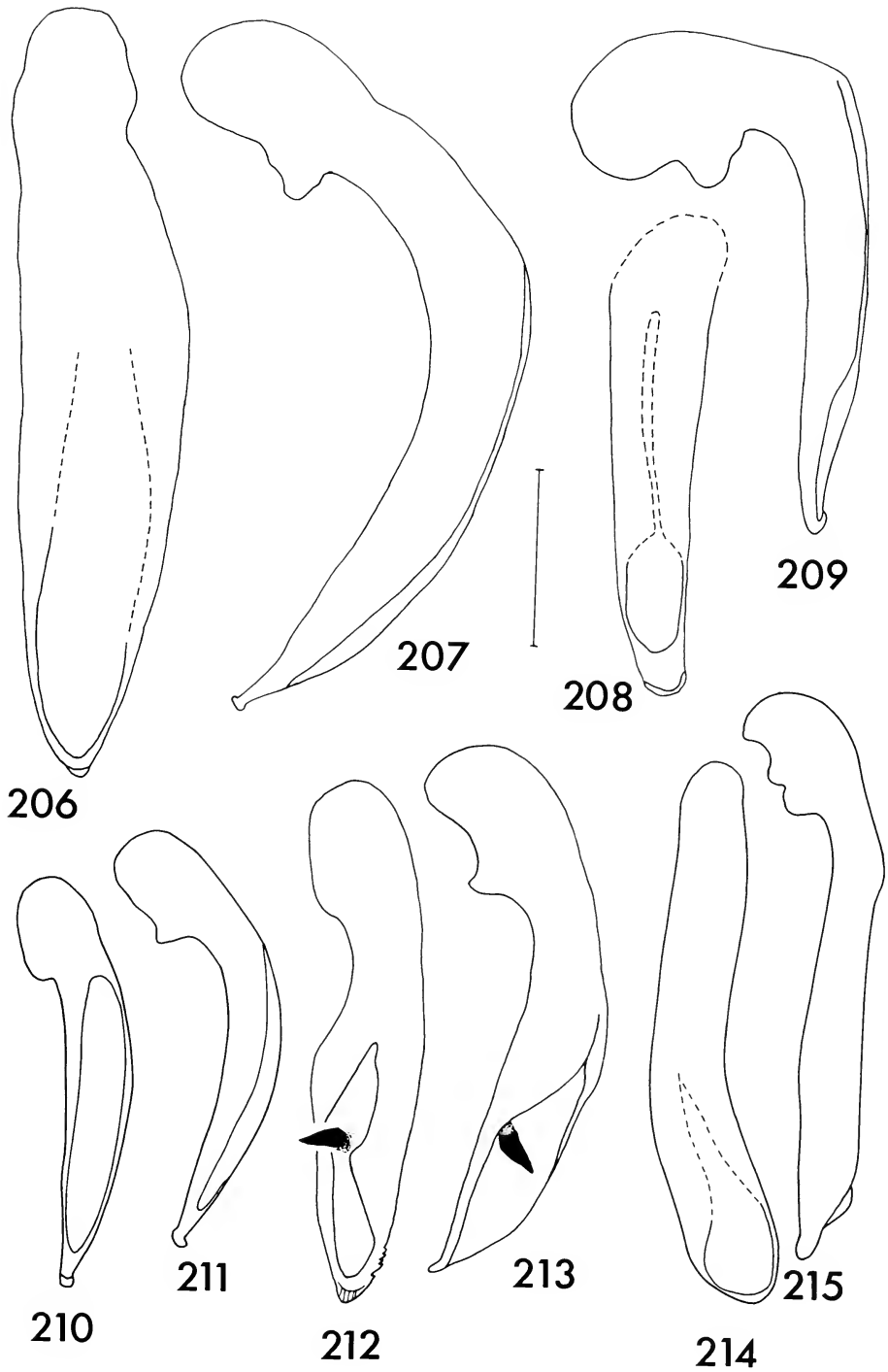
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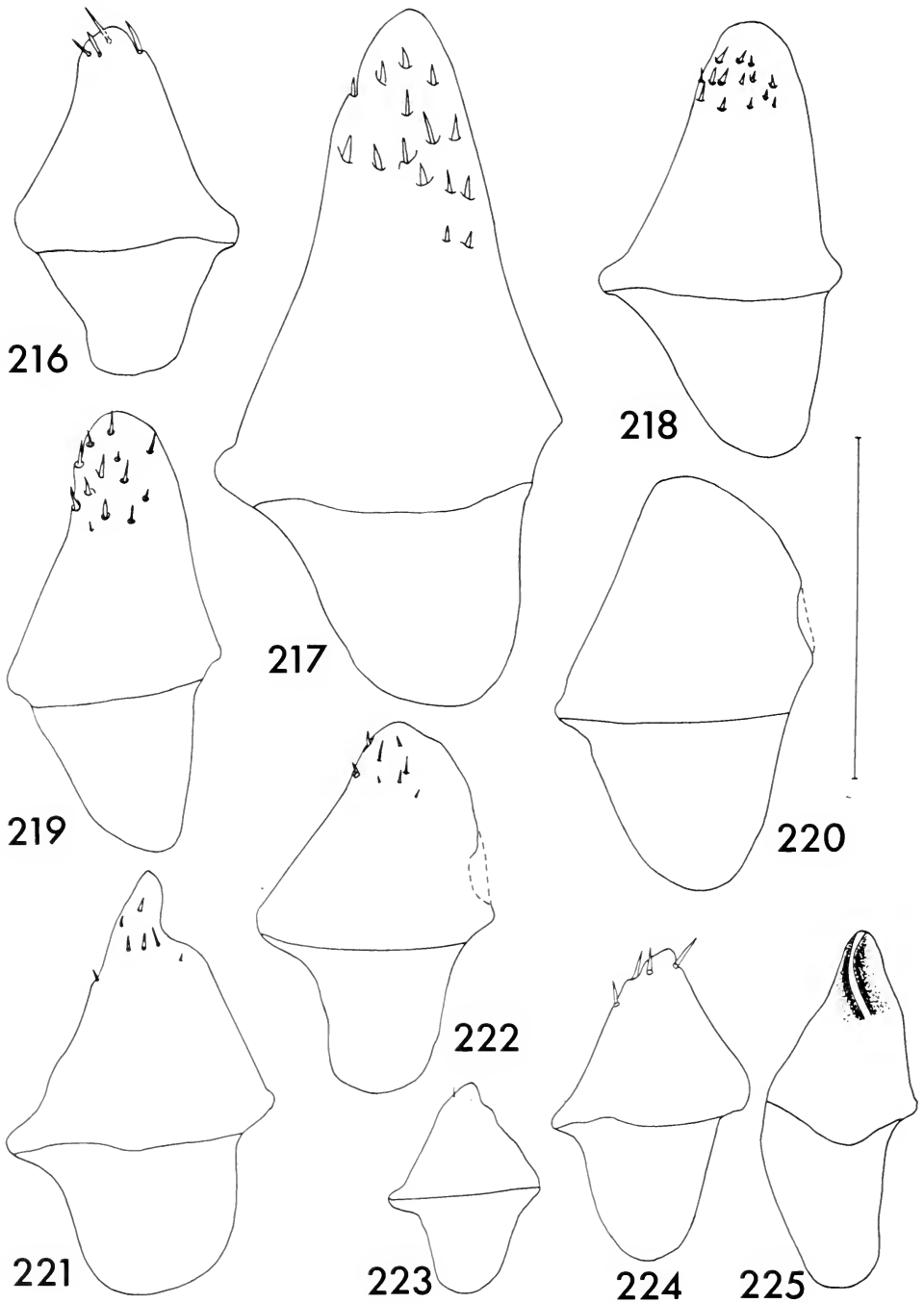
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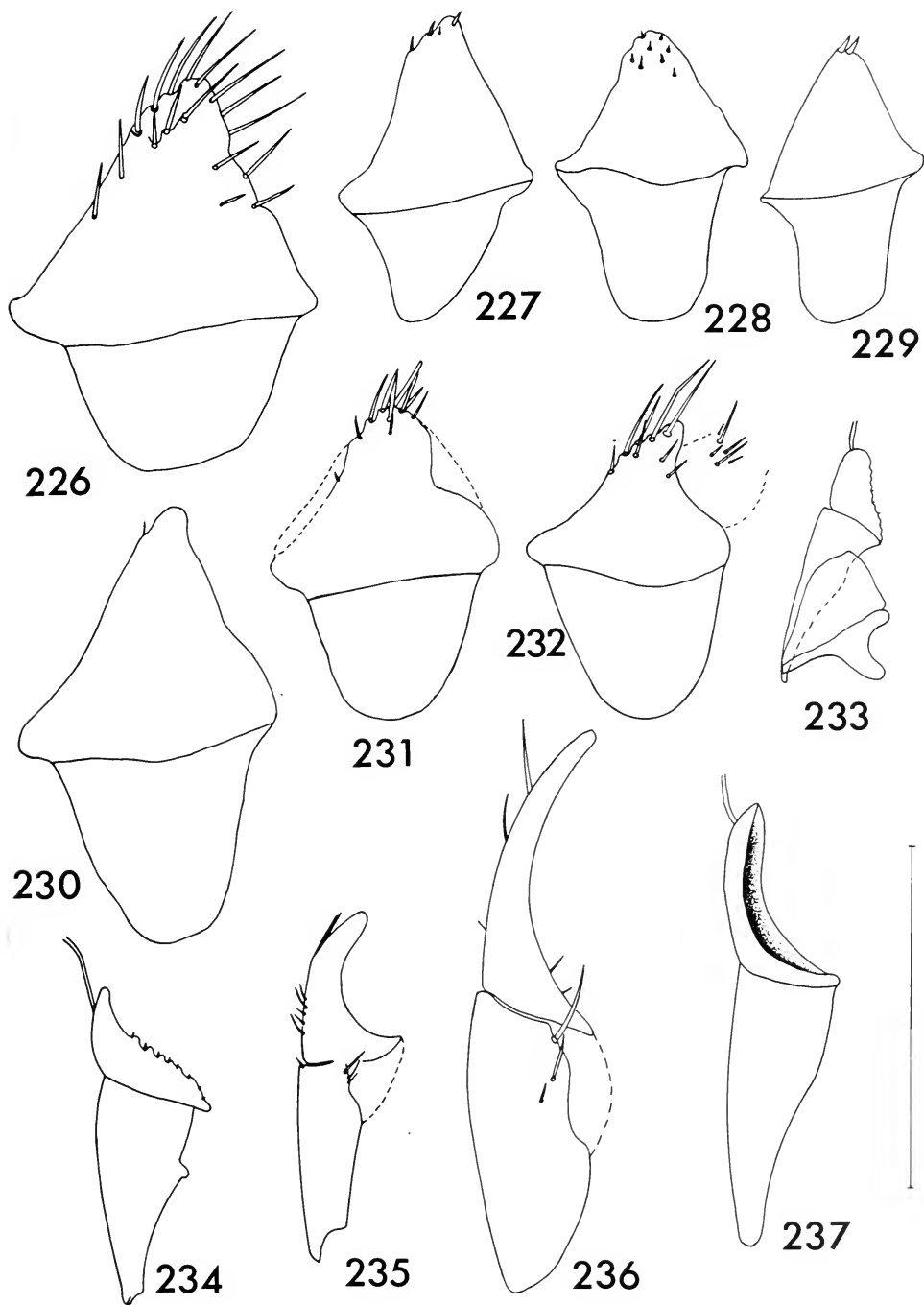
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Figs. 226-232. Valvifers of female genitalia, latero-ventral aspect. 226. *Geopinus incrassatus*. 227. *Xestonotus lugubris*. 228. *Diachromus germanicus*. 229. *Amphasia (A.) interstitialis*. 230. *Anisodactylus (Spongopus) verticalis*. 231. *Gynandromorphus etruscus*. 232. *Cenogmus castelnaui*. Fig. 233. Stylus and valvifer of female genitalia of *Amphasia (Pseudamphasia) sericeus*, latero-ventral aspect. Figs. 234-237. Stylus of female genitalia. 234. *Amphasia (A.) interstitialis*, latero-ventral aspect. 235. *Cenogmus castelnaui*, ventral aspect. 236. *Geopinus incrassatus*, latero-ventral aspect. 237. *Anisodactylus (A.) binotatus*, latero-ventral aspect. (scale line 1 mm).

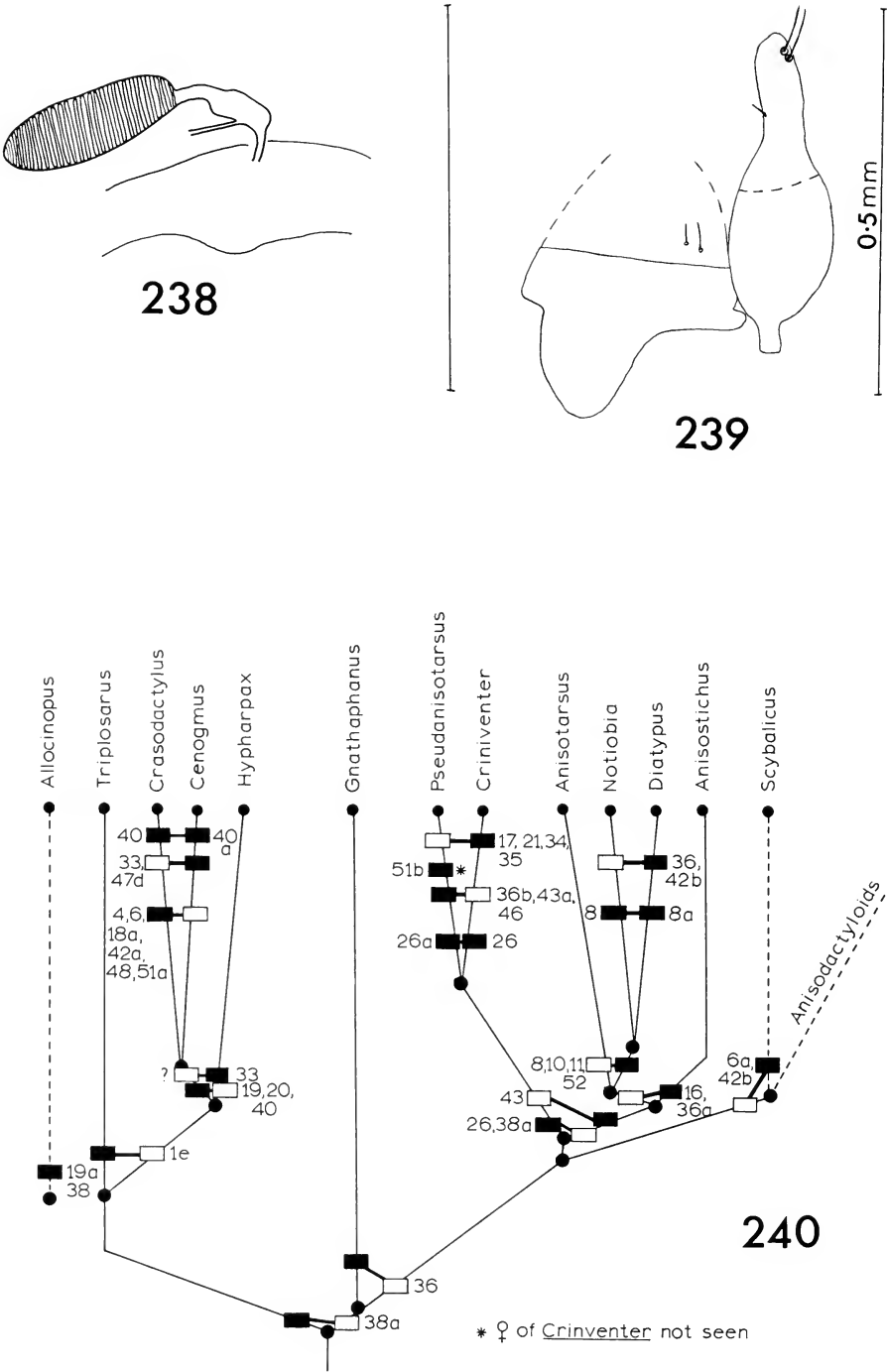


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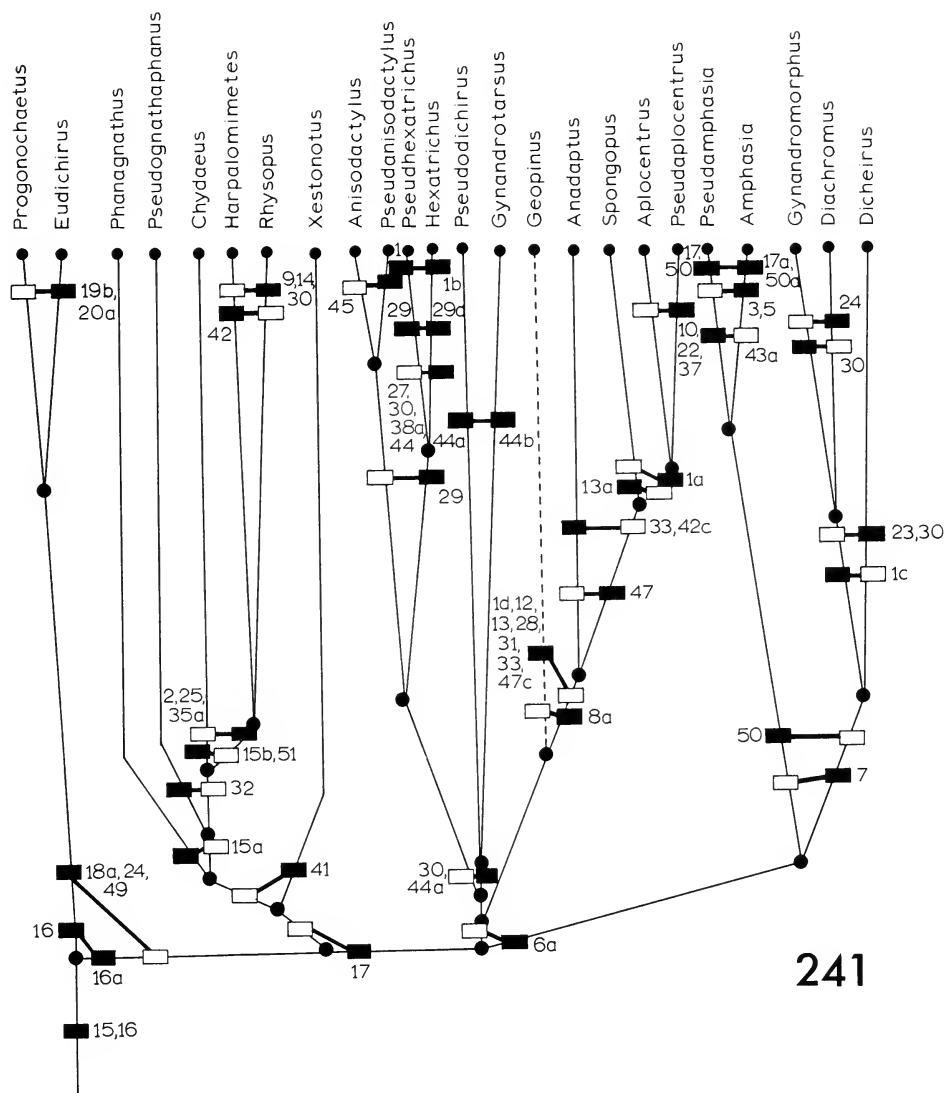


Fig. 241. Phylogeny of the Anisodactyloidea main branch of the subtribe Anisodactylina.

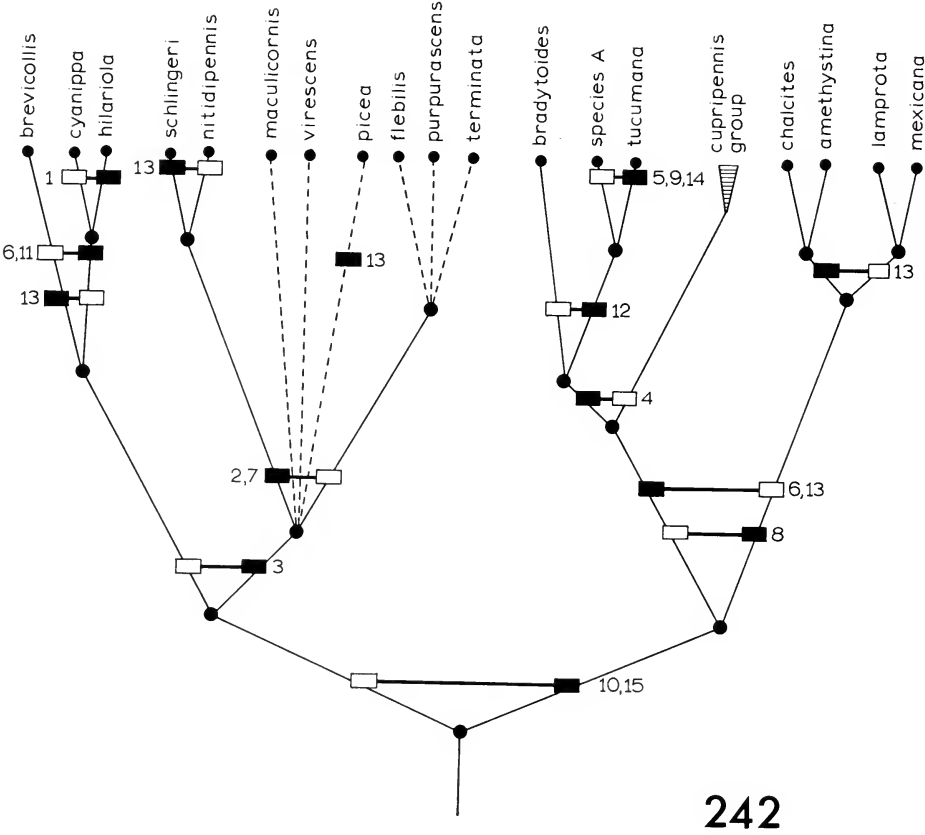


Fig. 242. Phylogeny of the New World species of the subgenus *Anisotarsus* (genus *Notiobia*).

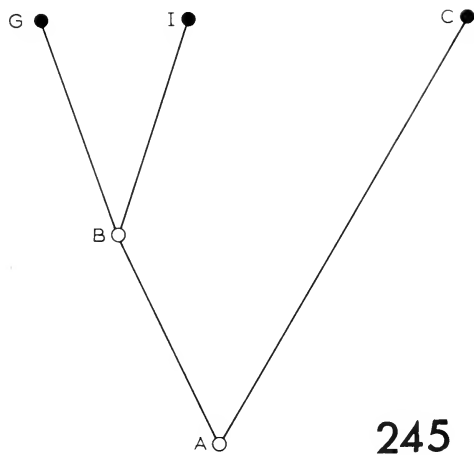
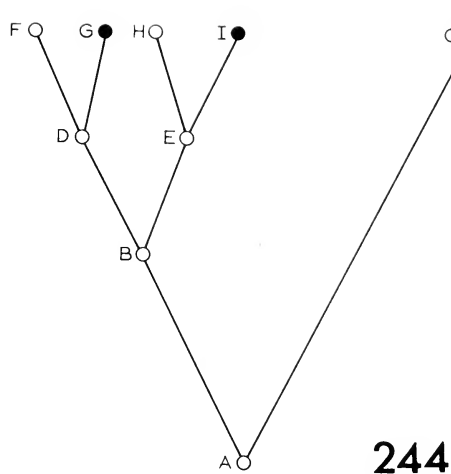
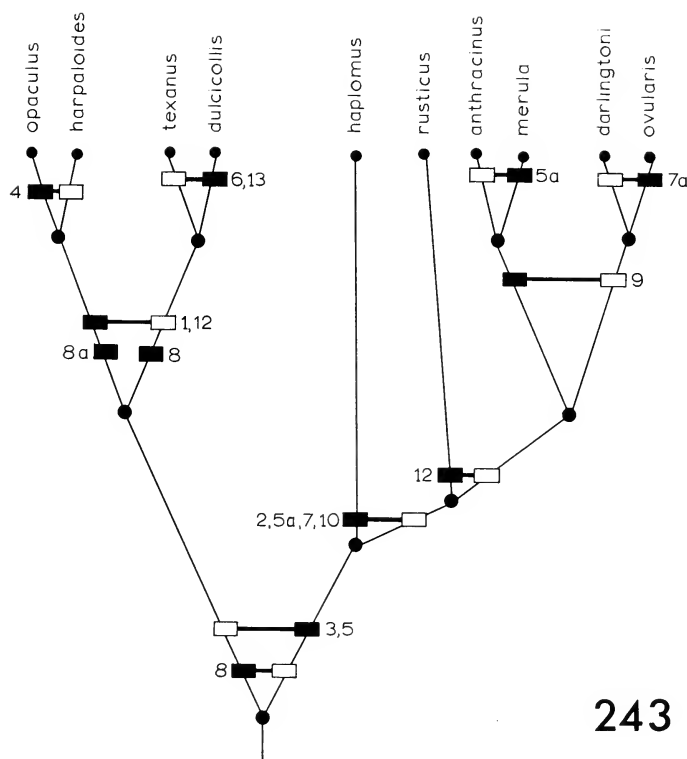
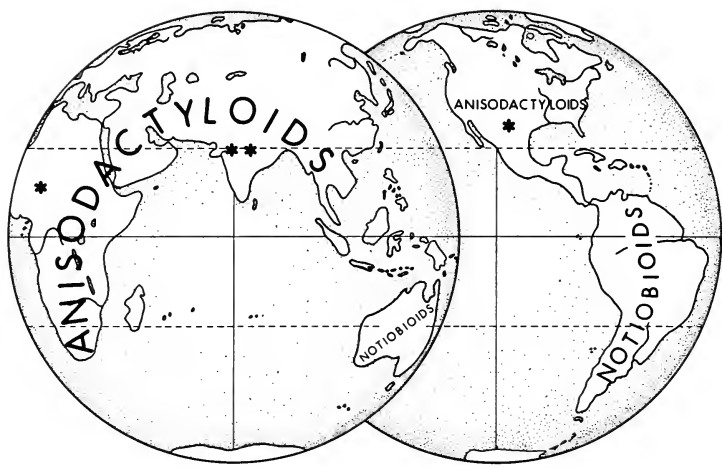
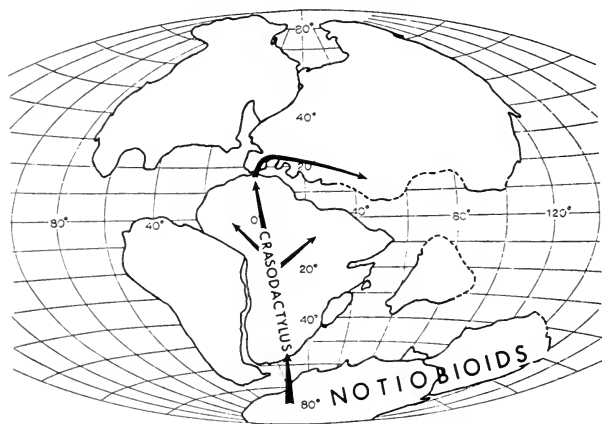


Fig. 243. Phylogeny of the species of the subgenus *Gynandrotarsus* (genus *Anisodactylus*). Figs. 244 & 245. Phylogenies of a hypothetical group of organisms (extinct forms represented by circles, extant forms represented by solid dots). 244. The actual phylogeny of the hypothetical group. 245. The phylogeny of the hypothetical group as reconstructed by a worker dealing only with extant forms.

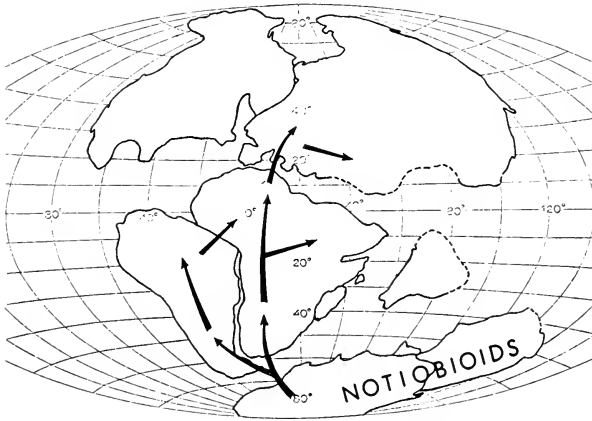


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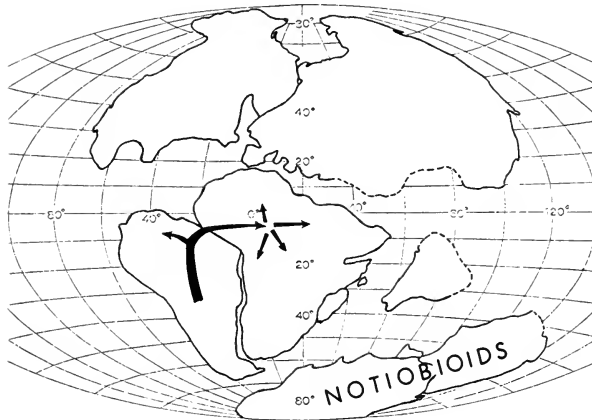


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Fig. 246. Contemporary distribution of the Notiobioid and Anisodactyloid main branches of the subtribe Anisodactylina (\* genus *Notiobia* of the Notiobioids also present in North America and Africa; \*\* genus *Scybalicus* of the Notiobioids also present in northern Africa and temperate Eurasia). Fig. 247. Postulated crossing in later Jurassic or early Cretaceous of ancestor of *Crasodactylus* to Africa and dispersal to Eurasia (map adapted from Dietz and Holden, 1970).

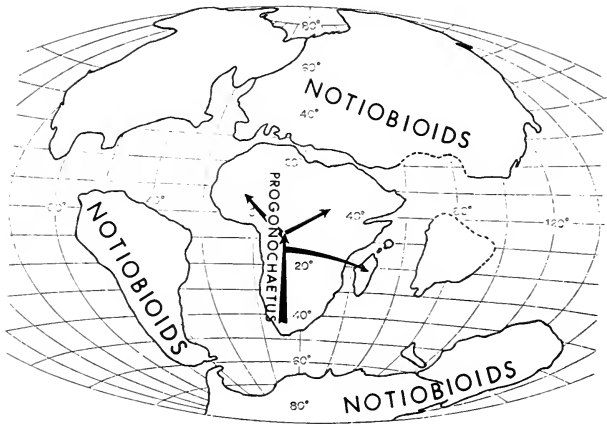


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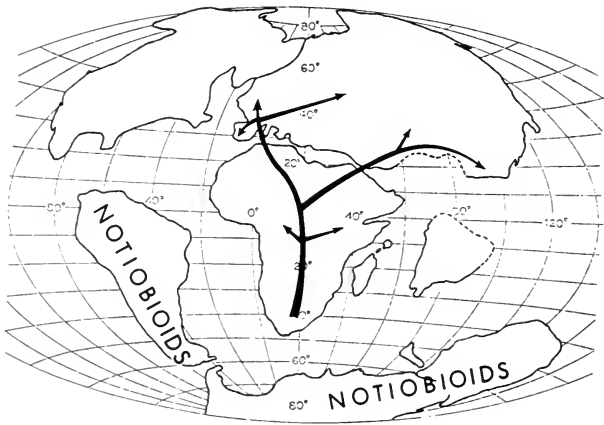


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Fig. 248. Postulated crossing of member of plesiomorphic *Notiobia* sub-branch in late Jurassic or early Cretaceous to combined continents of South America and Africa and subsequent dispersal northward to combined continents of Eurasia and North America (map adapted from Dietz and Holden, 1970). Fig. 249. Postulated spread of tropical adapted *Notiobia* sublineage throughout tropical portions of northern South America and subsequent crossing into Africa during Cretaceous (map adapted from Dietz and Holden, 1970).

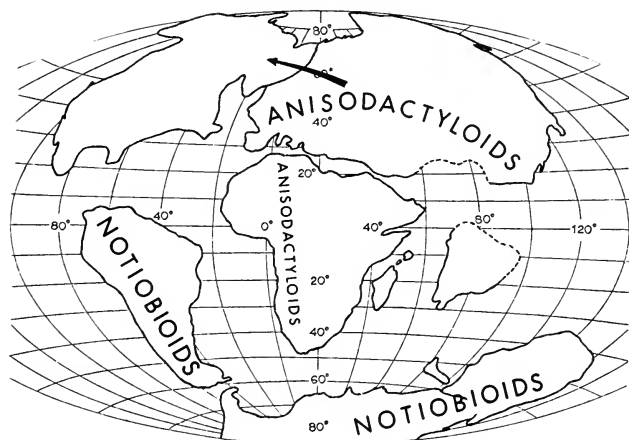


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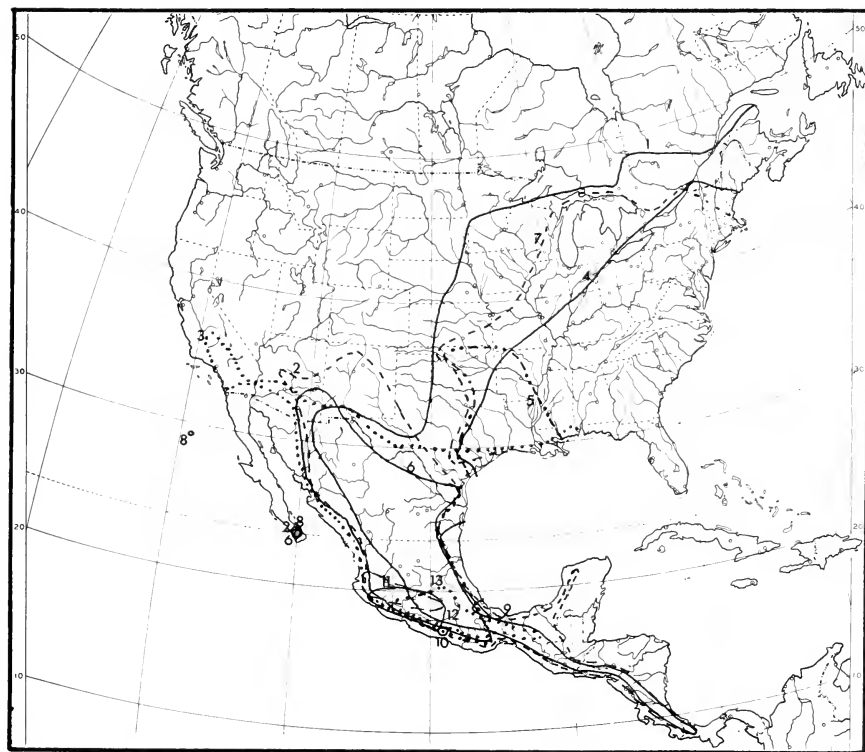


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Fig. 250. Postulated movement northward of first tropical adapted branch of Anisodactyloids to give rise to genus *Progonochaetus* in tropical Africa (map adapted from Dietz and Holden, 1970). Fig. 251. Postulated movement from temperate Africa of second tropical adapted branch of Anisodactyloids and displacement of most Notibioids from Africa and Eurasia (map adapted from Dietz and Holden, 1970).

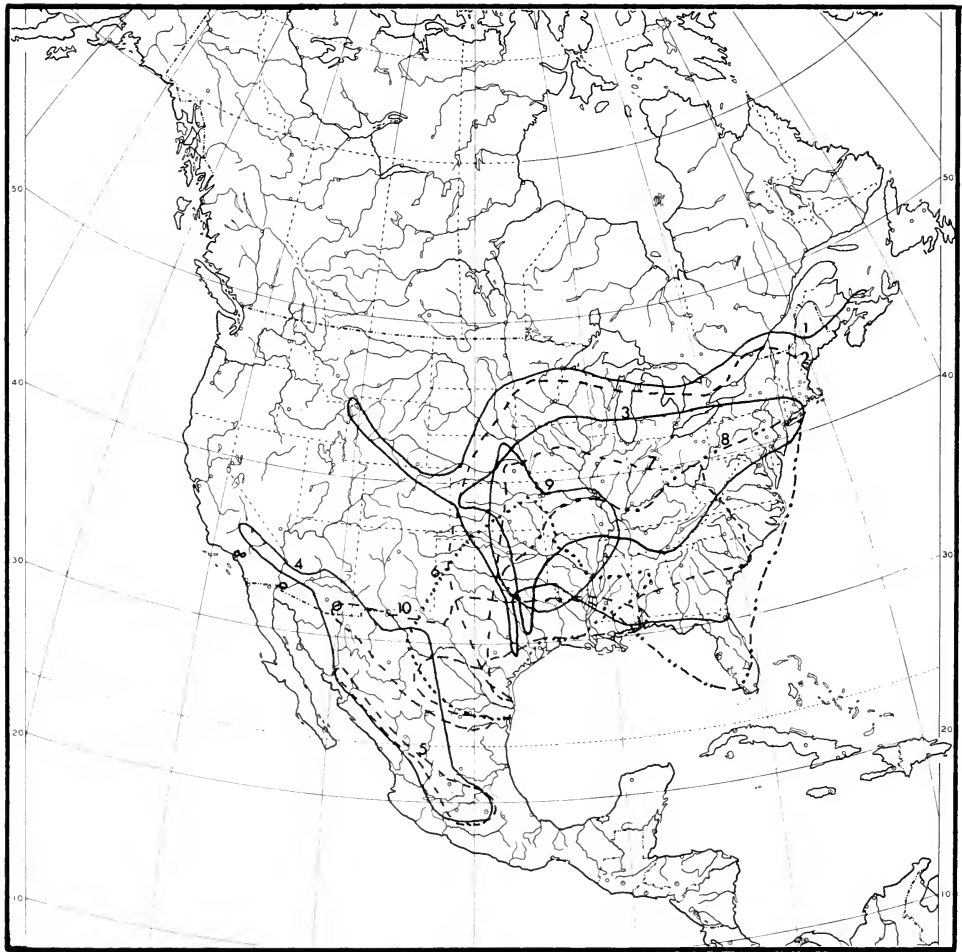


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Fig. 252. Postulated crossing of Anisodactylines into North America via the land connection with western Eurasia, subsequent extinction of any Notiobioids then present in North America (map adapted from Dietz and Holden, 1970). Fig. 253. Outlined ranges of North American species of the subgenus *Anisotarsus* (genus *Notiobia*). Numbers on map refer to species as follows: 1 - *terminata*. 2 - *mexicana*. 3 - *purpurascens*. 4 - *nitidipennis*. 5 - *maculicornis*. 6 - *brevicollis*. 7 - *picea*. 8 - *flebilis*. 9 - *lamprota*. 10 - *hilariola*. 11 - *cyanippa*. 12 - *schlingeri*. 13 - *virescens*.



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Fig. 254. Outlined ranges of species of the subgenus *Gynandrotarsus* (genus *Anisodactylus*). Numbers on map refer to species as follows: 1 - *rusticus*. 2 - *merula*. 3 - *ovularis*. 4 - *anthracinus*. 5 - *darlingtoni*. 6 - *opaculus*. 7 - *dulcicollis*. 8 - *haplomus*. 9 - *harpaloides*. 10 - *texanus*.





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